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Ambulatory dispersal of *Typhlodromus (Anthoseius) recki* Wainstein (Acari: Phytoseiidae) along Solanaceae stem

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Abstract

Tomato crops are attacked by several pests, including mites. While the main predatory mites are not effective enough to control mite pests due to problems with plant dispersal and establishment (associated with glandular trichomes - GT - on leaves and stems), recent studies have shown encouraging results with the European endemic phytoseiid *Typhlodromus (Anthoseius) recki*. The first objective of the present study was to assess the ability of this species to disperse along the tomato stem, considering six genotypes of *Solanum lycopersicum*, *S. peruvianum* and *S. cheesmaniae* with contrasted trichome numbers and types of stem trichomes, accurately characterised in a previous study. As morphological variation in body size has been observed within the species *T. (A.) recki*, the second objective was to determine how predator morphological traits can explain dispersal along the tomato stem. For this, ambulatory dispersal ability of females was tested in lab conditions on the eight *Solanum* genotypes. Then, the females were mounted on slides and body dimensions measured. No effect of the tomato genotypes was observed on the dispersal ability of the predator. However, specimens that succeeded in crossing the stem, had a higher mobility time than those that failed. Furthermore, body width at midbody and dorsal shield length were negatively correlated with dispersal ability. This suggests that the more slender and relatively small the specimens, the more are mobile and able to successfully cross the stem, regardless of the plant genotype considered. The number of glandular trichomes type (GT) VI and to a lesser extent GT I and IV, and non-glandular trichomes (NGT) II&III appear to limit dispersal. The GT VI seems to have a repellent effect, inducing mite escape in some cases. On the opposite, the number of NGT V were positively correlated with high mobility and stem crossing rates. Assuming that the main barrier to biological control efficiency is dispersal along tomato stems, the results obtained here should have implications for biological control success. The proportion of mites with 'optimal dimensions' appears to be low and further studies should be undertaken to better assess the proportion of mites with such ideal dimensions in different populations and also to determine whether these morphological traits are associated with different feeding abilities and/or abiotic conditions.

Introduction

Tomato crops are attacked by several pests, including mite pests as *Tetranychus urticae* (Koch), *T. evansi* Baker & Pritchard and *Aculops lycopersici* (Tryon). Their control is still mainly based on pesticide application, especially sulfur (with partial efficiency), because of the inability of their main natural enemies (predatory mites of the family Phytoseiidae) to cope with tomato trichomes and thus to disperse and then feed on prey (Van Haren et al. 1987). Trichomes are well known plant defense mechanisms that limit herbivory (i.e., Glas et al. 2012, Bar and Shtein 2019, Karabourniotis et al. 2020). Among species of the genus *Solanum* as well as among genotypes of a given plant species, trichome types are very diverse (i.e., glandular (GT) vs non glandular (NGT), small vs large, secreting toxic and/or repellent compounds) (i.e., Simmons and Gurr 2005). Numerous studies have been carried out on the effect of tomato leaf trichomes on pests, generally showing negative effects of GTs, especially types I and IV, which affect pest survival both through physical effects (trapping on sticky trichome tips) and

toxic and repellent effects due to the production of acylsucroses or terpenoids (Snyder et al. 1998, Chatzivalsileiadis et al. 1999, Kroumova and Wagner 2003, Fridman et al. 2005, Simmons and Gurr 2005, Economou et al. 2006, Treutter 2006, Gershenzon and Dudareva 2007, Alba et al. 2009, Glas et al. 2012, Dias et al. 2013, Lucini et al. 2015, Andrade et al. 2017, Rakha et al. 2017, Karabourniotis et al. 2020). Only a lower number studied the impact of such plant structures on natural enemies. Nevertheless, several authors have shown clear detrimental effects on several species of the predatory mite family Phytoseiidae. These authors emphasised the barrier effect of trichomes on the stem, preventing dispersal of predators throughout the plant and thus hampering biological control. GTs VI, which release toxic substances on contact with the mite, are the main types of trichomes that alter phytoseiid dispersal (Van Haren et al. 1987, Nihoul 1994, Cedola et al. 2001, Kennedy 2003, Sato et al. 2011, Van Houten et al. 2013, Davidson et al. 2016, Paspati et al. 2021, Castañé et al. 2022, Pandey et al. 2023). As a result, none of the commercial Phytoseiidae mite species are effective enough to control mite pests on tomatoes, leading to numerous attempts to develop new biological control solutions. The Phytoseiidae mite family comprises more than 2,500 species world wide (Demite et al. 2024). Some of these species are currently reported in Solanaceae, particularly in the genus *Solanum*, suggesting that these mites may be adapted to plant defenses. Most of these predator species are reported in the Neotropical region, where the genus *Solanum* originated, but also where the diversity of Phytoseiidae is the highest (Tixier et al. 2020a; Duarte et al. 2021). Because of potential problems related to ecological risks associated to the introduction of exotic species, studies have recently focused on endemic species from Europe collected on Solanaceae. Three species were particularly highly reported- *Typhlodromus (Typhlodromus) athiasae* Athias-Henriot, essentially occurring in Israel; *Phytoseiulus persimilis* Athias-Henriot, because of mass-release in tomato crops of this commercialised species; and *Typhlodromus (Anthoseius) recki* Wainstein widely reported all over Europe (Tixier et al. 2020a, Demite et al. 2024). Recent laboratory studies have shown that the latter species is able to feed on tomato mite pests and is therefore considered a promising predator (Tixier et al. 2020b, Ersin et al. 2021). The first objective of this study is to assess the ability of this species to disperse ambulatory along the tomato stem, considering six varieties of *Solanum lycopersicum*, *S. peruvianum* and *S. cheesmaniae* with contrasting types and densities of trichomes on stem. Some authors hypothesized that dispersal ability on tomato stem can be associated to mite size (Pijnakker et al. 2022). Observations of many specimens of *T. (A.) recki* have revealed large variations in body size (Tixier et al. 2021), suggesting a large intraspecific polymorphism, as has been observed in other Phytoseiidae species whose body dimensions vary with season, temperature and diet (Chant 1955, Tixier et al. 2003, Walzer and Schausberger 2011, Walzer et al. 2020). Therefore, the second objective of the present study was to determine whether the body size of *T. (A.) recki* could be related to the success of the mite in crossing the plant stem, for the eight tomato genotypes considered.

Material & methods

Plant material. Eight genotypes were studied: *Solanum cheesmaniae* (LA1412), *Solanum peruvianum* (Peru CMV) and six varieties of *S. lycopersicum* (747, Wooly, Yellow Bells, Clomimbo, Lancaster, Hairless). These genotypes were the same as those previously used for assessing the effects of

trichomes on leaf, stem and petiole on *T. urticae* and *T. (A.) recki* (Tabary et al. 2024). To obtain the experimental plants, seeds were sown in plastic pots (8 x 8 x 8 cm) in a greenhouse (25 ± 2°C, 40 ± 30% RH) and watered twice a week until the beginning of the experiment (when plants reached three leaves).

Mite Material. The mite stock colony of *T. (A.) recki* was initiated from populations (50–100 specimens) collected on *Phlomis fruticosa* L. (Lamiaceae) at Saint Clément-de-Rivière (Hérault, France, 43.694144, 3.851792) on July 2021. Predatory mites were reared following the process described by McMurtry and Scriven (1965), in rearing units constituted of plastic arenas (10 x 15 cm) deposited on moistened sponge support, surrounded by water-saturated paper tissue for avoiding mite escape. The population was maintained in a climatic chamber (25 ± 2°C, 16D:8N photoperiod, 70 ± 30% RH) and fed with commercialized *Typha angustifolia* pollen (Nutrimite®) twice a week.

Trichome characterization. The trichome characterization followed the protocol used by Tabary et al. (2024) on the same plant material. Briefly, a piece of 1 cm of stem between the second and third leaf was cut with a razor blade, and on two areas of 4 mm² the types and number of trichomes were evaluated using a stereomicroscope (Nikon SMZZ1500 (x20)). Two replications were performed per plant, and 5 plants of each genotype were evaluated (in total 10 replicates / genotype). The trichome type classification proposed by Luckwill (1943) and Channarayappa et al. (1992) were used. The trichomes types I, IV, V and VI were considered separately, while types II and III were grouped together due to their similarity and the lack of studies demonstrating their role in arthropod resistance (McDowell et al. 2011). Trichome types VII and VIII were not taken into account due to their rarity on the eight genotypes studied.

Experimental design. A 5 cm stem piece, located between the second and third leaf, was cut with a razor blade and then disposed on wet cotton on a Petri dish. A bean leaf disc (2.5 cm diameter, cv. Contender) with pollen of *T. angustifolia* (Nutrimite®) was disposed at one extremity, whereas a small piece of black plastic was placed at the other extremity (Fig. 1). One young mated female of *T. (A.) recki* was then disposed on the plastic piece. Once the female has dispersed on the stem, the plastic piece was removed. At least 10 replicates were carried out for each genotype. The age of predatory females was the same for each replicate. Observations were carried out at four different times: 10 minutes, 25, 55 and 100 minutes after the predator introduction. At each observation time, the predator was filmed for 5 minutes (camera Leica EZ4 W) and several parameters were assessed during the video observations: (i) the success of stem crossing : number of predators reaching the bean leaf and not turning back, (ii) hesitation behavior : the number of times the mite goes on and turns back on the stem without totally crossing it, (iii) escape behavior: number of predators retrieved on the wet cotton support and (iv) the mobility vs immobility duration. At the end of the experiment, the females were mounted on slides in Hoyer's medium. The mites were then observed using a microscope (Leica DLMB, Leica Microsystemes SAS, Rueil Malmaison, France) (400 x magnification), and body dimensions were measured. The Dorsal Shield Length (DSL) was assessed by measuring the distances between the setae *j1* and *J5*. Three Dorsal Shield Width (DSWs) were assessed: (i) at the fore hind part measuring the distances between

the setae *z4* (DSW1), (ii) at the median part measuring the distances between the setae *s6* (DSW2) and (iii) at the backward part measuring the distances between the setae *S5* (DSW3) (Fig. 2).

Typhlodromus (A.) recki body size phenotypes. Tixier et al. (2021) carried measurements of 91 females of *T. (A.) recki* collected on six plant species in France and in Italy. Among the characters considered, these authors measured the dorsal shield length and although the measurements were not taken at exactly the same positions on the body as in the present study, DSL (measured at the edge of the body tegument in Tixier et al. (2021) and between setae *j1* and *J5* in the present study) and DSW1 (measured at the edge of the body tegument at the level of setae *z3* in Tixier et al. (2021) and between setae *z4* in the present study), we decided to use this dataset to determine whether the populations under consideration had variable body sizes and the proportion of “small” individuals in each of these populations.

Statistical analyses. All analyses were carried out using R Cote Team (2021). ANOVA were carried out to assess the mean differences in mobility time and hesitation numbers between the *Solanum* genotypes and between the females that succeed to cross or not the stem. ANOVA were also carried out to determine based on the dataset of Tixier et al. (2021) differences in DSL and DSW1 between the populations of *T. (A.) recki* here considered. ANOVA was carried out using the Kruskal-Wallis test (package “rstatix”) followed by Dunn test when the data did not follow a Normal law and/or with different variances, otherwise ANOVA tests (package “car”) followed by Newman & Keuls test (package “Agricolae”) were performed. A multifactorial analysis was used to assess the relationships between trichome numbers, mite body size and mobility time variables, using the packages “FactoMineR” and “factoextra”. Correlation tests (corr.test) were also carried out to determine the relationship between the three dorsal shield dimensions using the package “ggpubr”.

Results

Trichome characterization of the *Solanum* genotypes. The multifactorial analysis, which explains 35.2% and 23.6% of the variability for axes 1 and 2 respectively, shows that stem GT VI and NGT V differentiate the genotypes most (Fig. 3a, b). On the axis 1, the density of these two trichome types were negatively correlated to the density of GT I, NGT II&III and GT IV on the axis 1. On the axis 2, the density of trichome GT IV, GT VI and NGT II&III was positively correlated to each other and differentiated from that of trichome GT I and NGT V. The genotypes were included into two main groups: (i) comprising *Solanum peruvianum*, *S. cheesmaniae* and *S. lycopersicum* cv. Hairless: characterized by high densities of NGT V, GT VI and low densities of trichomes GT I, NGT II&III and GT IV, and (ii) comprising *S. lycopersicum* cv. Woolly, cv. Yellow Bells and 747, characterized by opposite density of these latter trichome types. The cultivar Clomimbo and Lancaster had an intermediate position.

Typhlodromus (A.) recki ambulatory dispersal ability. Predatory mites succeeded to cross the stem for five genotypes among the eight considered. However, the success crossing rate was low, except for *S. peruvianum* (Fig. 4). The mean numbers of “hesitation” was not different between genotypes ($P = 0.73$).

No significant difference was either observed in the numbers of “hesitation” between the females that succeed to cross or not the stem ($P = 0.56$). The percentage of mobility duration was not significantly different between the eight genotypes, all along the experiment and for each date except at 10 minutes, where a higher mobility activity was observed on *S. peruvianum*. At all times measured, the time spent moving was longer for females that succeeded to cross the stem than for those that did not (Fig. 5).

A multifactorial analysis was carried out, considering the mean values of trichome stem density of each genotype, dispersal predator parameters and its body size. The axes 1 and 2 represented 58.7% of the total variability of the system (Fig. 6). Mobility time variables correlated with each other, as well as with hesitation numbers and crossing success rates, suggesting that the more mobile females were, the more hesitation numbers (forwards and backwards) were high, and the more stem crossing success was important. These walking parameters were positively and negatively correlated with the number of trichome NGT V and GT VI, respectively, suggesting that the density of GT VI had a negative effect on dispersal, whereas the density of NGT V had no effect. In a lesser extent, the numbers of trichomes GT I, NGT II&III and GT IV were also negatively correlated with the mobility ability, suggesting that the numbers of these trichome types may also act as a barrier for predator ambulatory dispersal along the stem. The escape rate was positively associated to the number of GT VI, but not to the densities of GT I, NGT II&III and GT IV, suggesting that the presence of trichomes GT VI might be repellent for the predator. Predator mortality is not related to stem trichome characteristics and only little explains the variability in the system. Dispersal parameters were negatively correlated with dorsal shield length (DSL) and width, especially at the central body part (DSW2), suggesting that the smaller the mite length and width, the higher the mobility time, number of hesitations and crossing success. Finally, mites with a rather small and narrow body size were associated with stems with a low number of GT VI and, to a lesser extent, with GT I, NGT II&III and GT IV, suggesting that mites with such dimensions would be better able to cope with tomato trichome defenses.

Variability of *T. (A.) recki* body dimensions. The analyses were conducted on the dataset produced by Tixier et al. (2021). The mean DSL and DSW were significantly different between the populations of *T. (A.) recki* and the plants where they were collected. The lower dimensions were observed for specimens collected on *Cirsium arvense* L. (Compositae) and *Echium vulgare* L. (Boraginaceae), whereas the highest were observed from specimens collected on *S. lycopersicum*, *Datura* sp. (Solanaceae) and *Mentha suaveolens* L. (Lamiaceae); the specimens collected on *P. fruticosa* showing an intermediate position (Fig. 7). These measurements were not exactly the same as those considered here, as they were taken at the boundary of the body and not between the setae, so their values are higher. Nevertheless, the Fig. 8 shows a correlation between these two measurements ($R = 0.53$, $P < 0.0001$). The proportion of small and narrow specimens was the highest for specimens collected on *C. arvense* and *E. vulgare*.

Discussion

The present study indicates that a relationship exists between types and numbers of trichomes on the stem and the ambulatory dispersal behavior of *T. (A.) recki*, observed during a short period of time (110

minutes). The NGT V on the stem was not associated to plant defense and high numbers of this trichome type even favor the mobility of the predator, as already observed for various pest species (Onyambus et al. 2011, Keskin and Kumral 2015, Savi et al. 2019). The density of GT VI affected the most *T. (A.) recki* mobility. This result is consistent with observations already reported for other Phytoseiidae mite species (Van Haren et al. 1987, Paspati et al. 2021), whereas contrasted effects of the density of GT VI on the leaf were observed for the prey *T. urticae* (Onyambus et al. 2011, Rakha et al. 2017, Savi et al. 2019, Kortbeek et al. 2021). For example, in Phytoseiidae mites, Paspati et al. (2021) showed detrimental effects of GT VI on the dispersal of the mite *Amblyseius swirskii* Athias-Henriot due to the toxic effect of acylsugars causing (i) suffocation due to acylsugar accumulation at mite cuticle openings and (ii) disruption of the subcuticular membrane (Puterka et al. 2003). Here, the mortality of the predator was not different between plant genotypes, regardless of the number of GT VI. The cuticle of *T. (A.) recki* is quite sclerotized (Livshitz and Kuznetsov 1972) compared to that of other Phytoseiidae species, and especially *A. swirskii*. This morphological trait could explain the lack of effect of trichome exudates on the mortality of *T. (A.) recki*, but the relatively short observation period could also explain the low mortality here observed. Further experiments will help to confirm if *T. (A.) recki* can cope with the toxicity of acylsucrose. The density of GT VI was also correlated to the numbers of hesitation and escape rates. A repellent effect, causing the mites to move on and then turn back, could be hypothesized, as has already been observed for pest mites (Maluf et al. 2001) and Phytoseiidae mites (Sato et al. 2011). The density of the other trichome types (GT I and IV, and NGT II&III) was also associated with low mobility and stem crossing, but to a lesser extent than GT VI. The GT I and IV are reported to be detrimental for pests when present on leaves (i.e., Simmons and Gurr 2005). Here, GT I and IV do not seem to be related to escape. This suggests that, unlike trichome VI, they do not have a repellent effect. The effect of NGT II&III was rather unexpected, as studies even ignore this trichome type when examining the effects of trichomes density on arthropods. Most of these later studies concern the leaf surface, we can thus hypothesize a different effect of these trichomes when present on the stem. However, we cannot rule out the possibility that such an effect of NGT II&III may also be due to an artefact, since plants with high densities of GT I and IV also have high densities of NGT II&III.

The present study provides new information on the dispersal behavior of predators, showing that mobility time and "hesitation" activity (walking forward and backward) are both related to stem crossing success. This suggests that the predator is trying to cross the stem in an incisive way, and the more it tries, the more it succeeds. Van Haren et al. (1987) showed that the dispersal of predators is facilitated when the pest mites have crossed the stem, as the passage of the prey causes trichome breakage and loss of toxicity over time. Van Houten et al. (2013) reported that dispersal of *A. swirskii* is favored on stems attacked by *A. lycopersici*, due to trichome collapse after the pest passage. To our knowledge, whether such trichome collapse and loss of toxicity occurs after predator passage is not known. It would therefore be interesting to determine whether the "stubbornness" of *T. (A.) recki* individuals observed in this study could be linked to a strategy aimed at facilitating the dispersal of the rest of the colony, by carrying out similar experiments with a large number of specimens of the predator.

Although only a small proportion of the total number of *T. (A.) recki* examined managed to cross the stem (15%), there were correlations between mite size and crossing success / mobility activities. The mite size parameters that were the most related to stem crossing were the dorsal shield length and the mid-body width and to a lesser extent fore hind and back widths. These results seem to show that the smaller and narrower the mite specimens, the higher the stem crossing success. Several authors have in the past suggested a relationship between mite size and ability to squeeze through trichomes, especially for the tydeid mite *Pronematus ubiquitus* (McGregor) (Ilionidae), and for some mite pests as the eriophyid mite *A. lycopersici* (Pijnakker et al. 2022). However, these mite species are much smaller than *T. (A.) recki* (even than specimens that succeeded to cross the stem). The Phytoseiidae mites studied until now are usually bigger than *T. (A.) recki*, especially for *A. swirskii* and *P. persimilis*, *P. longipes* and *P. macropilis*. In addition, these predatory mites issued from commercial rearings are usually well fed, so their size is significant and their ability to spread through trichomes is likely to be difficult. It will therefore be necessary to test the success of stem crossing as a function of body size in other mite species and for other stages such as immatures and males. Tixier et al. (2021) showed different morphological phenotypes of *T. (A.) recki* depending on the plants from which the populations were collected. Using this latter dataset, differences in the length and width of the dorsal shield were observed between these populations, with the smallest specimens found more frequently in the populations collected on *E. vulgare* and *C. arvense*, the population collected on *P. fruticosa* (the one used for the present experiments) having an intermediate position. It would therefore be interesting to carry out experiments similar to the present ones, using the other *T. (A.) recki* populations, in order to validate the hypothesis that the size of the mites and the success of stem-crossing are related, i.e. that the mite crossing rate is higher for mites collected on *E. vulgare* and *C. arvense* and lower for mites collected on *M. suaveolens*, *S. lycopersicum* and *Datura* sp.

Conclusion

The present study confirms the detrimental role of stem trichome density in the dispersal of Phytoseiidae mites, especially GT VI, which also seems to have a repellent effect. It also shows that females try hard to cross the stem, and the more mobile they are, the higher the success rate. These results open new avenues for biocontrol, in particular to determine whether this behavior can be linked to trichome collapse, which subsequently might facilitate the passage of other specimens. Noteworthy relationships between predator body size and stem crossing success were also found. The proportion of stem-crossing specimens within the population studied here is quite low, but other populations, than the one currently considered, appear to have a higher proportion of small specimens. Thus, additional studies would be required to test the stem crossing success of specimens from these latter populations. Several factors can affect mite size, as climatic conditions and plant phenotypes (Chant 1955, Tixier et al. 2003, Walzer et al. 2020). Thus, although the present study highlights new potential traits for selecting the predator phenotype best adapted for dispersal along the tomato stem, further experiments are needed to determine how much predator size is labile and how much is determined by environmental factors. It would also be necessary to determine the extent to which feeding behavior differs between

small and large predator phenotypes for issues of biological control efficacy. Finally, this study mainly focuses on mite size, but other characters may also be involved in crossing success, as mite dorsal sclerotization which is particularly well developed in *T. (A.) recki*, in contrast to the other Phytoseiidae species tested so far.

Declarations

Author Contribution

Marie-Stéphane Tixier, Maria Navajas and Denise Navia defined the experimental design. Amandine Raeckelboom, Martial Douin and Lou Tabary carried out the experiments. Amandine Raeckelboom and Marie-Stéphane Tixier carried out the statistical analyses. Marie-Stephane Tixier wrote the manuscript with Maria Navajas and Denise Navia.

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Figures

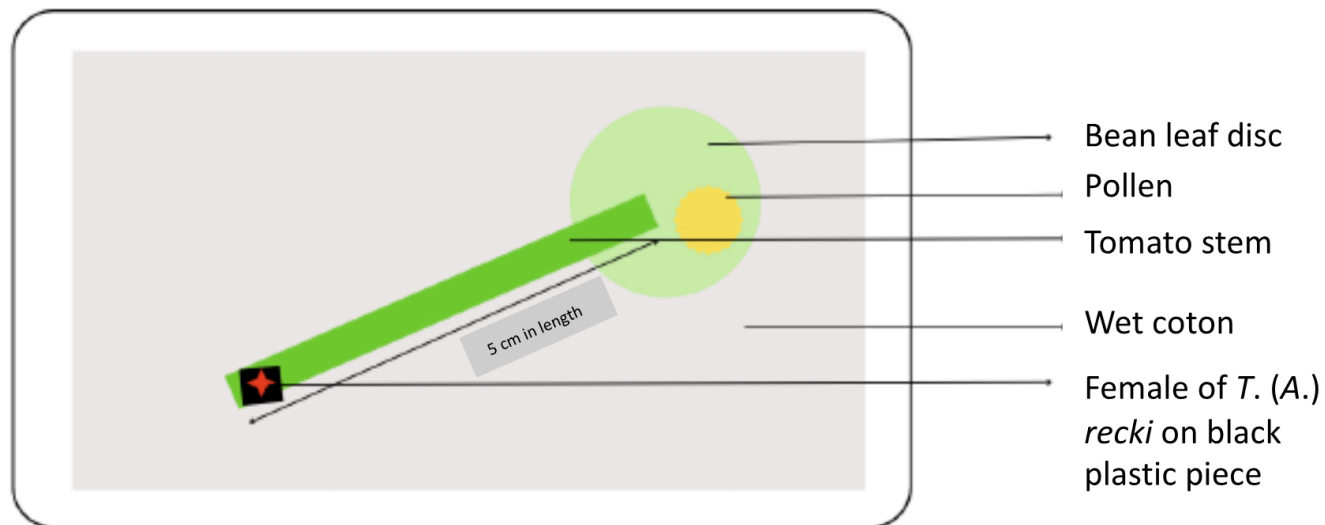


Figure 1

Schema showing the experimental design to study the movement of *T. (A.) recki* on the stem of six varieties of *S. lycopersicum*, and *S. cheesmaniae* and *S. peruvianum*

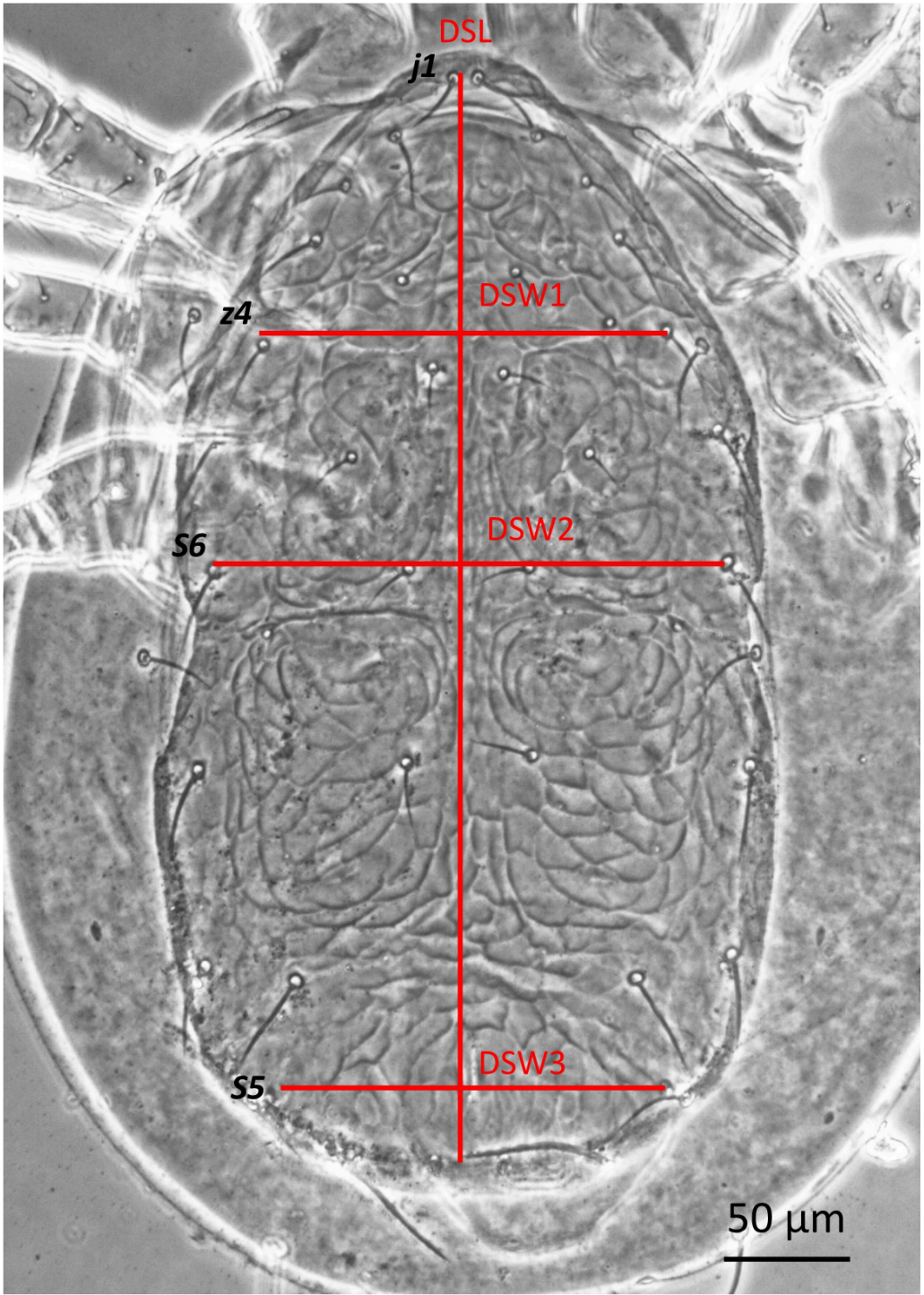


Figure 2

Schema showing body dimensions measured on specimens of *T. (A.) recki*

(a)

(b)

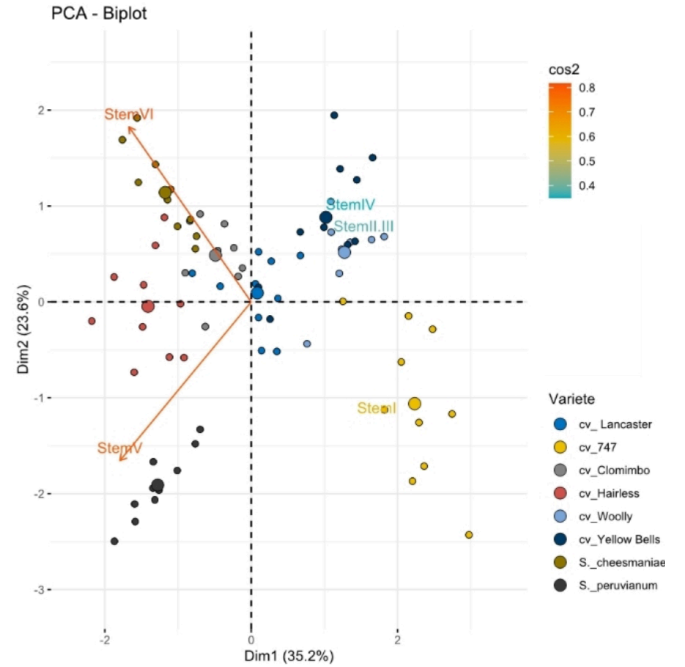
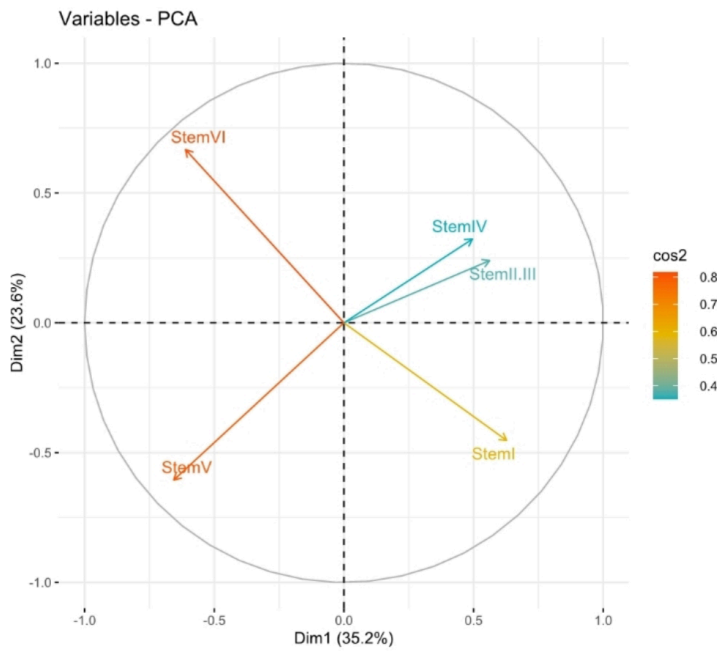


Figure 3

Results of the multifactorial analysis considering trichome density on stem of on the six *Solanum lycopersicum* varieties, *S. peruvianum*, *S. cheesmaniae* : (a) correlation circle and (b) biplot showing both variables and the projection of the genotypes considered.

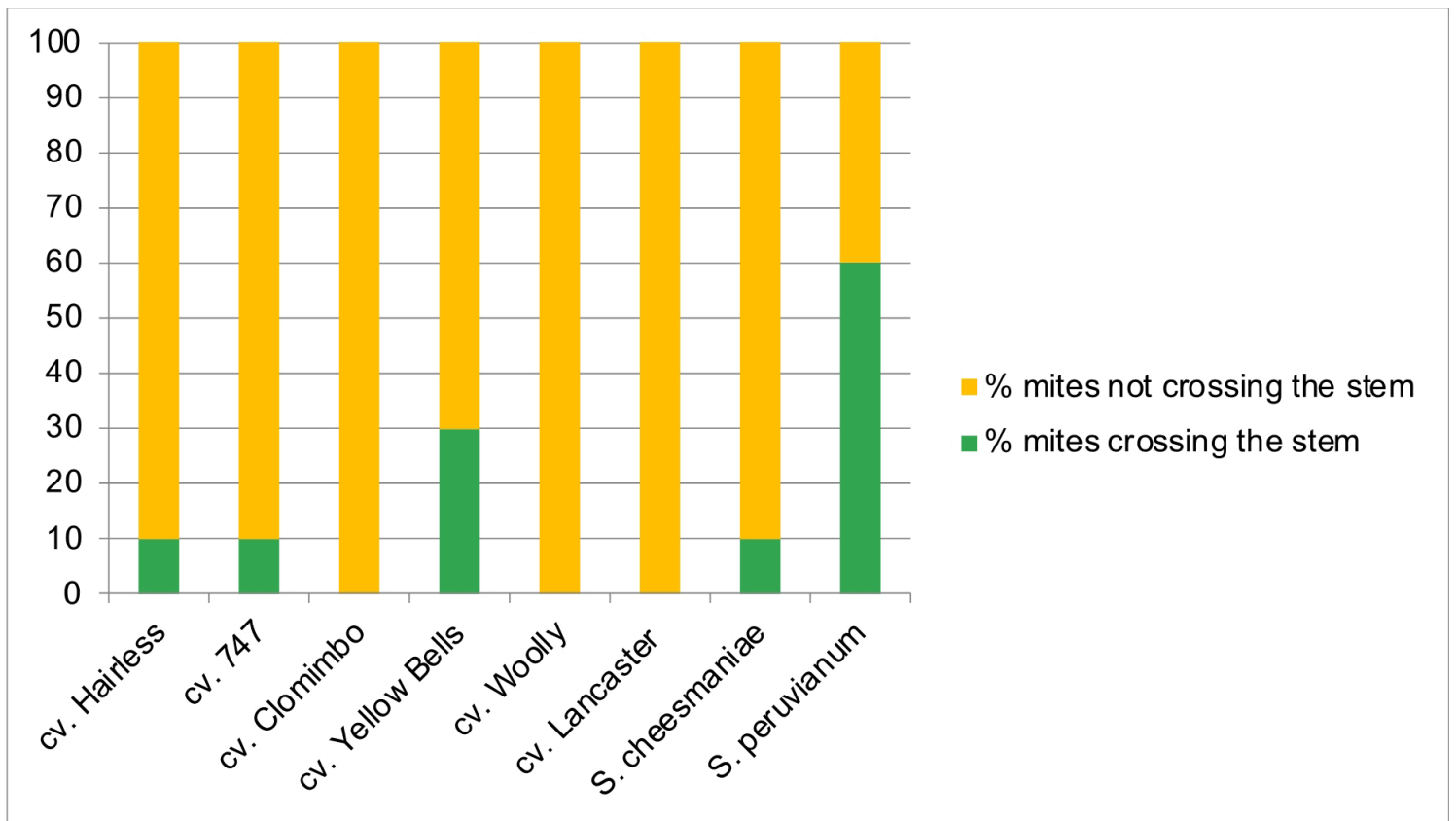


Figure 4

Percentage of females having or not crossed the stem of the six varieties of *S. lycopersicum*, and *S. cheesmaniae* and *S. peruvianum*

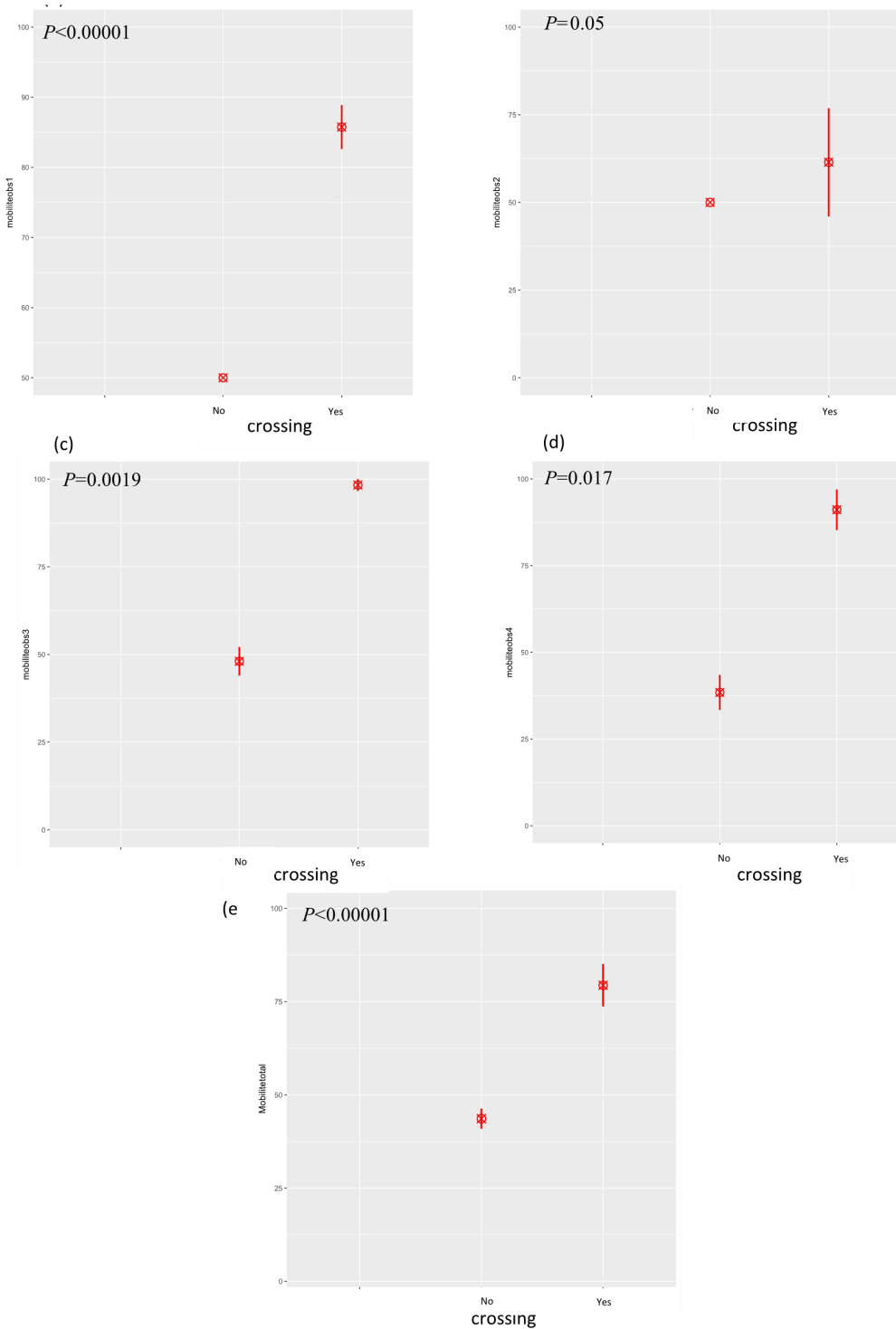
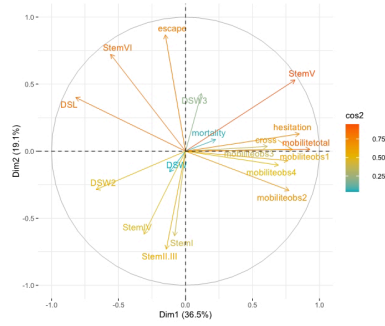


Figure 5

Mean number of *T. (A.) recki* crossing or not the stem during an observation period of: (a) 10 minutes, (b) 25 minutes, (c) 55 minutes and (d) 100 minutes after the predator introduction and (e) for the cumulated observation time (20 minutes).

(a)



(b)

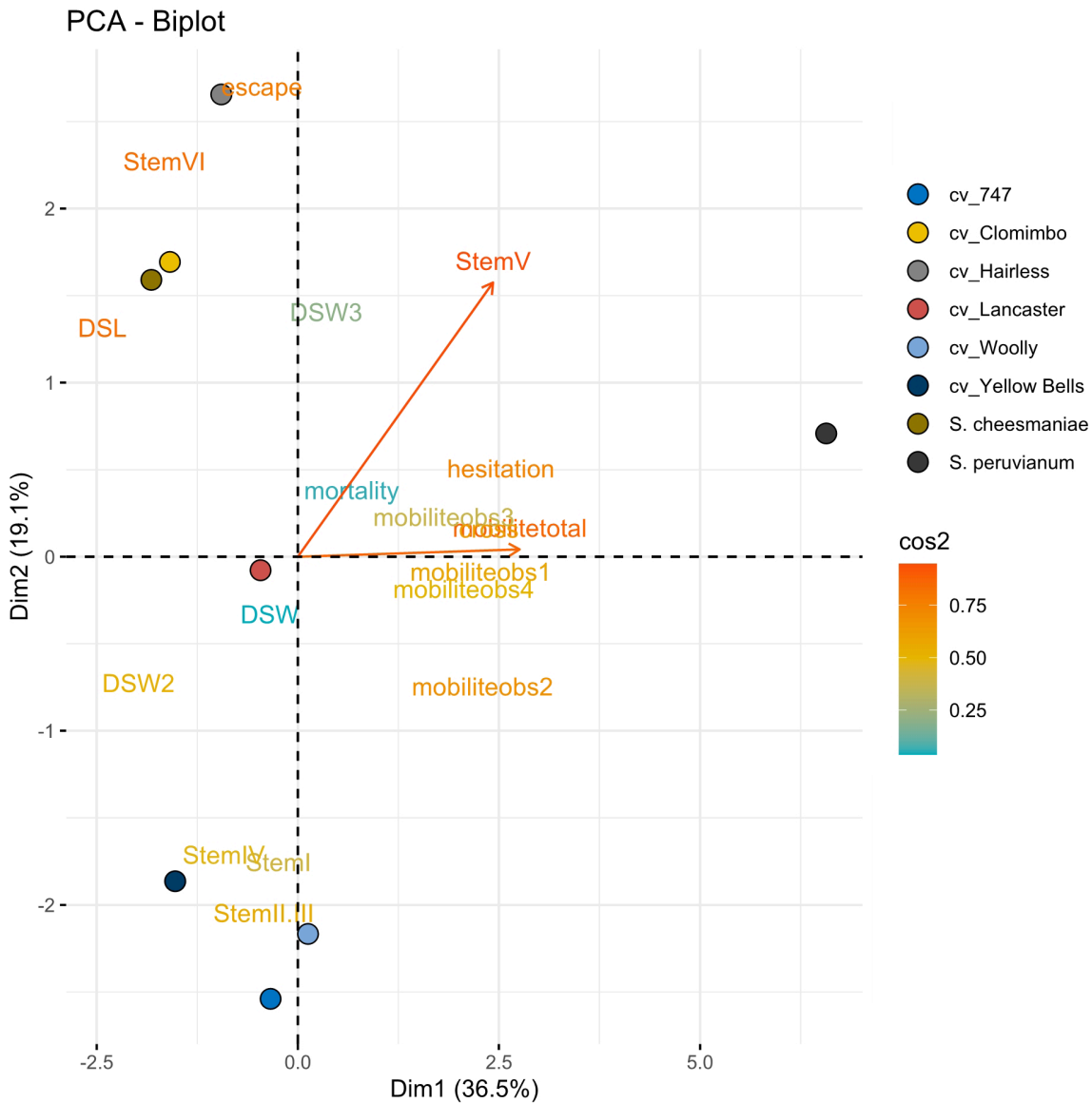


Figure 6

Results of the multifactorial analysis considering the mean dispersal variables of *T. (A.) recki*, the mean size of *T. (A.) recki* specimens and the mean number of each trichome types on the stem on the six *Solanum lycopersicum* varieties, and *S. peruvianum*, *S. cheesmaniae* (a) correlation circle and (b) projection of the mean data for the genotypes considered.

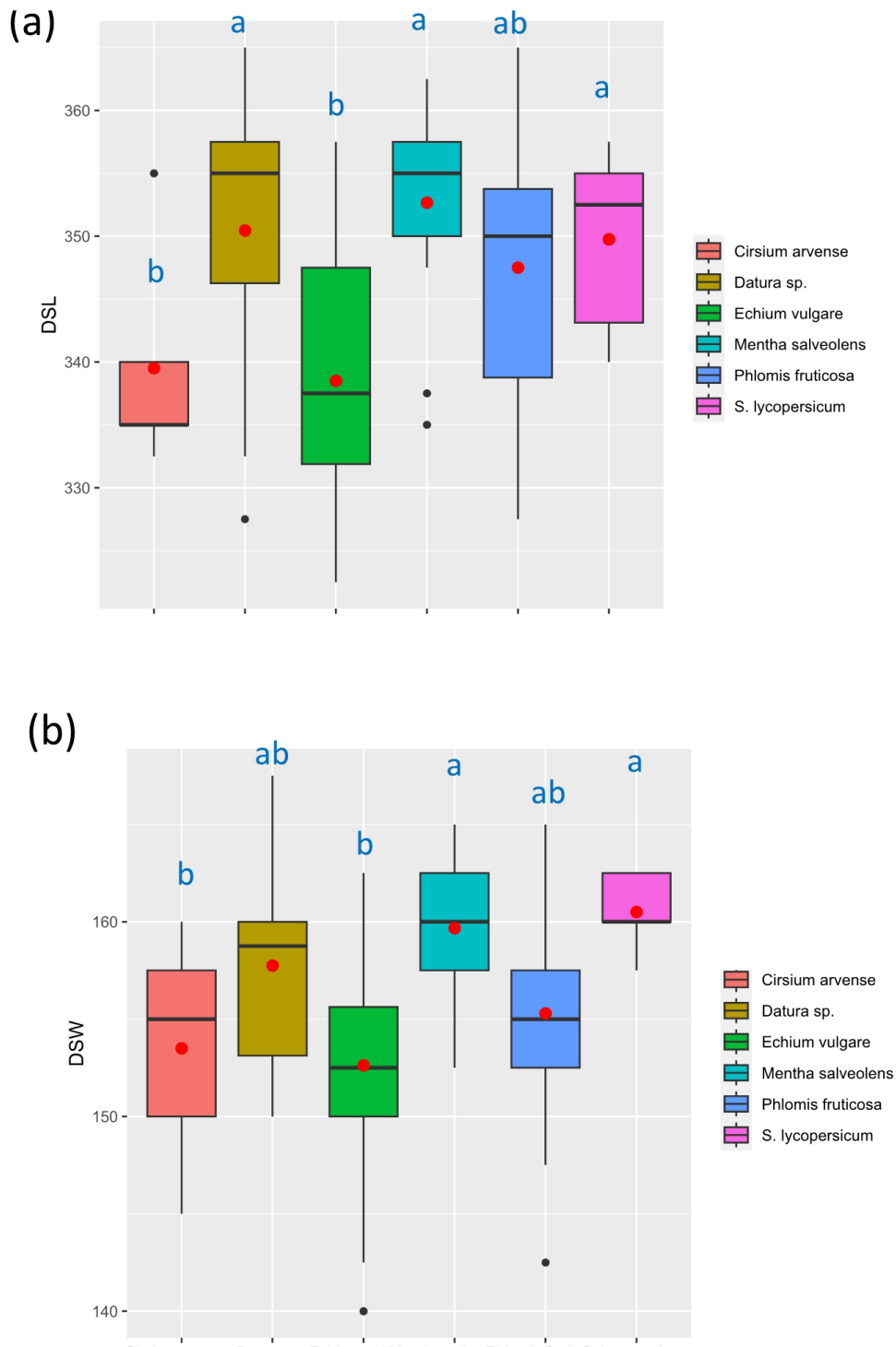


Figure 7

Boxplots showing (a) the mean number of dorsal shield length and (b) the dorsal shield width between specimens of *T. (A.) recki* collected on *Mentha suaveolens*, *Solanum lycopersicum*, *Datura sp.*, *Phomis fruticosa*, *Echium vulgare* and *Cirsium arvense* (dataset issued from Tixier et al. 2021). Letters correspond to results of the Newman & Keuls post-hoc test.

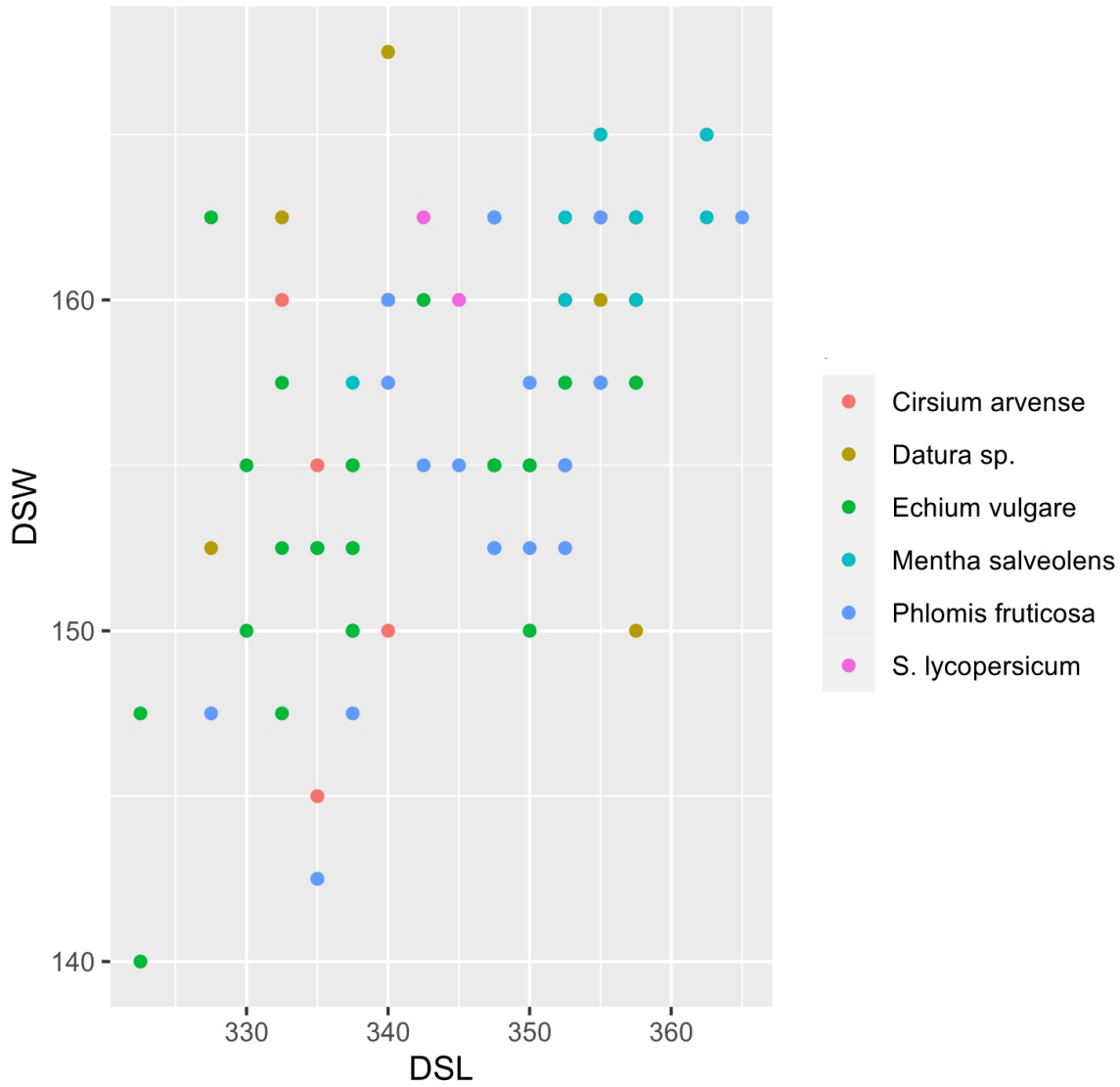


Figure 8

Relation between the Dorsal Shield Length (DSL) and Width (DSW) of specimens of *T. (A.) recki* collected on *Mentha suaveolens*, *Solanum lycopersicum*, *Datura sp.*, *Phomis fruticosa*, *Echium vulgare* and *Cirsiium arvense* (dataset issued from Tixier et al. 2021).