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Article

Preference of *Thrips tabaci* Lind. for *Allium cepa* L., *Allium fistulosum* L., and *Allium roylei* Stearn

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Abstract: *Thrips tabaci* Lind. (Thysanoptera: Thripidae) is a key pest of onions worldwide. It causes both direct and indirect damage to onion crops, resulting in high yield losses. Nowadays, the Integrated System of Production and Plant Protection requires onion growers to use onion thrips resistant cultivars. It has become apparent that improvement of already existing onion cultivars may not be a sufficient, so it is necessary to look for desirable plant traits related to disease and pest resistance among existing and wild cultivars. For this purpose, we conducted bioassays on the possible preference of *T. tabaci* for three different cultivars of *Allium cepa* L., namely, Alibaba, Bila, Tęcza, one cultivar Kroll of Welsh onion, *Allium fistulosum* L., and wild species *Allium roylei* Stearn. The settling preference and the oviposition rate of female onion thrips were evaluated using choice and no-choice laboratory tests, respectively. During the bioassay, on leaf sections of the *A. roylei* species, a significantly higher number of *T. tabaci* females was recorded compared to the cv. Tęcza of the *A. cepa* species and the cv. Kroll of the *A. fistulosum* species, in each observation period. Significantly more thrips settled on cv. Kroll compared to Alibaba and Bila. Regarding the results obtained on *A. cepa*, significantly fewer females were found on cv. Bila compared to cv. Tęcza. Opposite results were observed in a combination of cvs. Tęcza - Alibaba, where significantly more insects settled on leaves of cv. Alibaba. Statistically significant differences of cultivars/species were found in the number of hatched larvae on the leaves of the tested cultivars/species of onion. The significantly lowest number of larvae hatched from eggs laid on *A. roylei* compared to *A. fistulosum* and cultivars of *A. cepa*, except for Bila.

Keywords: bioassay; oviposition; settling preference; resistance

1. Introduction

Onion (common onion or bulb onion) (*Allium cepa* L.) is one of the most important vegetable crops worldwide with a global total production of 93,226,400 tones and it accounts for about 24% of the world's total vegetable production [1]. Onion production and breeding encounter many challenges. Like other crops, onions are susceptible to insect, fungal, bacterial, viral, and nematode pests [2,3]. One of the main insect pests is the onion thrips (*Thrips tabaci* Lind.; Thysanoptera: Thripidae). It is a phytophagous and polyphagous, invasive, cosmopolitan and highly fecundating insect pest with a rapid development rate, and vector of several onion pathogens and tospoviruses [4-8]. Attack by *T. tabaci* not only leads to a complete loss of onion seedlings but also may cause damage to older crops by feeding on leaves as well as onion bulbs [9]. The poor effectiveness of insecticides at controlling thrips – and thrips' increased resistance to them – leads to high losses in the cultivation of onions [10,11]. A reduction in yield of about 40-65% has been reported due to attacks by these pests [12,13]. Full resistance (or tolerance) of onion to *T. tabaci* would be very beneficial, however, in the available literature, we have not found information about the existence of such cultivars and breeding lines of onion. However, in recent years, some plant characteristics that are responsible for the partial resistance of onions to *T. tabaci* have been identified. The differences in

resistant and susceptible cultivars have been associated with leaf color [14], amounts and types of epicuticular leaf wax [15,16], plant architecture and anatomy [17,18] and total phenol content [19,20]. Recently, it was also possible to select some onions genotypes that showed a lower number of thrips compared to susceptible ones [19,21], and those produced large bulb yields under thrips pressure [17,22]. Onion breeding programs currently focus mainly on the improvement of existing cultivars; however, wild *Allium* species possess many desirable traits such as disease and pest resistance [23].

Allium roylei Stearn and *Allium fistulosum* L. have been recognized as the most important gene pools of onion [24,25]. *A. roylei* is a wild species originating from the Indian subcontinent which possesses genes imparting resistance to various harmful fungal diseases and pests [26-29]. *A. fistulosum* (Welsh onion, Japanese bunching onion, spring onion) is widely cultivated in Japan, China and Korea. Its origin is unknown; it is believed to be of Chinese origin [30]. This *Allium* sp. also possesses many traits agronomically useful for onions, due to its resistance to onion leaf blight, pink root, anthracnose, and onion fly [23,31,32].

Our previous field studies, in which *A. roylei* and *A. fistulosum* were less colonized and damaged by *T. tabaci* compared to *A. cepa* cultivars and breeding lines [33], encouraged us to continue research on them. Therefore, this research under laboratory conditions was conducted to prove *T. tabaci* settlement and oviposition activity on leaves of *A. roylei* and *A. fistulosum* compared to three cultivars of *A. cepa* that differed in their susceptibility to colonization and feeding of thrips under field conditions [20].

2. Materials and Methods

2.1. Test plants

Three onion species were used in the laboratory experiments: *Allium cepa* L. (cvs. Alibaba, Bila and, Tęcza.), *Allium fistulosum* (cv. Kroll), and *Allium roylei* (ecotypes 333). All the *A. cepa* and *A. fistulosum* cultivars used in the trials are recommended for cultivation in central Europe and are commercially available. The seeds were obtained from Polish breeding companies, namely PlantiCo Zielonki in Stare Babice (cvs. Alibaba, Bila, and Kroll) and Spójnia in Nochowó (cv. Tęcza). *A. roylei* seeds we obtained from the bank Plant Genetic Resources Laboratory, Research Institute of Vegetable Crops in Skierniewice in Poland. The onion plants used in the experiments were grown in a standard substrate in trays within a plant growing room at $24 \pm 1^\circ\text{C}$, $35 \pm 5\%$ relative humidity and a photoperiod of 16:8 h light:dark. All plants were watered regularly, only with tap water. Leaves from onion plants that were approximately four weeks old were used in all bioassays.

2.2. Test insects

Using a rearing method adapted from Loomans & Murai (1997) [34], a stock culture of a thelytokous *T. tabaci* strain was maintained on white cabbage leaves in 0.75-liter glass jars covered with a fine mesh to ensure ventilation. The rearing was kept in a climate chamber at $24 \pm 1^\circ\text{C}$, $35 \pm 5\%$ relative humidity and a photoperiod of 16:8 h light:dark. White cabbage was purchased regularly, and fresh pieces of leaf were added two to three times a week.

To obtain groups of females of known age, thrips pupae were randomly collected from the rearing jars and transferred to Petri dishes (diameter 90 mm) with sections of leek (*Allium ampeloprasum* L.) leaves. The dishes were closed with lids with central holes covered with a fine mesh to allow air circulation and were sealed with sealing film to prevent the thrips from escaping. After 48 h, adult females were checked, and any remaining pupae were removed. Following an additional pre-oviposition period of 48 hours, single females were used in the bioassays.

2.3. Oviposition rate

The oviposition rate of female onion thrips on *Allium* species/cultivars was evaluated using a no-choice test. For this bioassay, four-centimeter sections of onion leaves were cut from the middle part of the leaves of the respective test plant. To protect the leaf sections from desiccation and to prevent the thrips from getting inside the leaves, both ends of the leaf sections were briefly dipped

in warm liquid paraffin wax. After the wax had solidified, the leaf sections were placed singly on a thin film of 1 % water agar (Agar – Agar, Kobe I, Carl Roth, Karlsruhe, Germany) in glass Petri dishes (60 mm diameter). Subsequently, single females of known age were transferred to each glass Petri dish and placed on the leaf section. To prevent the escape of the *T. tabaci* females, the dishes were covered with thin (14 µm) clear plastic film (Carl Roth, Karlsruhe, Germany), which was perforated (one hole per cm² on average) using insect pins (0.4 mm diameter). The bioassay units were kept in a climate chamber at 24 ± 1°C, 35 ± 5% relative humidity and a photoperiod of 16:8 h light:dark. After 24 hours, the females were removed. The plant sections with eggs were kept in the climatic chamber for another five days. After that, the hatched larvae were counted under a stereoscopic microscope.

2.4. Settling preference

The settling preference of *T. tabaci* females for leaf sections of the different *Allium* species/cultivars was determined by means of a choice test. Eight pairs of species/cultivars were compared against each other: Tęcza × Alibaba; Tęcza × Bila; Tęcza × Kroll; Tęcza × *A. roylei*, Alibaba × Bila; Alibaba × Kroll; Bila × Kroll; and Kroll × *A. roylei*. Each pair consisted of two four-centimeter sections of onion leaves, sealed with wax at both ends (as described above). These sections were placed parallel and equidistant to each other in the center of the bottom of a 90 mm diameter glass Petri dish. Subsequently, ten females of unknown age were placed at the starting point in the center, between the parallel-lying onion leaf sections of the tested pair of cultivars. Each bioassay unit was covered with perforated plastic film and completely randomized under an artificial light source in a climate chamber at 24 ± 1°C and 35 ± 5% relative humidity. Ten, 30, 60, 120, and 180 minutes after the female thrips had dispersed from the starting point, the number of thrips were counted on each of the two sections of onion leaves of the tested cultivars, as well as in the surrounding space. The experiment was replicated 10 to 12 times resulting in preferences recorded for 100 to 120 female thrips for each pair of onion cultivars/species.

2.5. Statistical analysis

Analyses of the bioassay data were performed using Statistica 13 software (TIBCO Software Inc., 2017). The results of the settling preference tests were analysed with Student's t-test with a significance level of $P < 0.05$. The data obtained from the oviposition tests with hatched thrips larvae were subjected to a one-way analysis of variance (ANOVA), with the factor onion cultivar/species. Residual plots were checked prior to data analysis. In cases where the data did not show a normal distribution, they were normalized by $\log(x+1)$ transformation. The Tukey test was used to compare means at a significance level of $P < 0.05$.

3. Results

In the no-choice experiments on the oviposition rate of female onion thrips, significant variability was observed among cultivars/species regarding the mean number of thrips larvae that had hatched from eggs laid inside the tissue of the onion leaves ($F = 27.158$; $df = 4$; $p < 0.000$). *T. tabaci* females laid significantly more eggs on leaves of *A. cepa* cultivars compared to *A. roylei* (almost three times more) (Figure 1). Additionally, a significantly higher number of *T. tabaci* larvae hatched from eggs laid on cv. Tęcza and Bila compared to *A. fistulosum* (cv Kroll). Moreover, a significantly higher number of *T. tabaci* larvae hatched from eggs on cv Kroll than on *A. roylei* (Figure 1).

In a preference test for onion thrips settling on different species and cultivars of *Allium* sp., a significantly higher number of female onion thrips settled on leaf sections of *A. roylei* compared to cv. Tęcza (*A. cepa*) and cv. Kroll (*A. fistulosum*) during each observation period (Figure 2c, d). In both comparisons, almost twice as many *T. tabaci* females were observed on leaf sections of *A. roylei*. When *A. cepa* cultivars were paired with cv. Kroll (*A. fistulosum*), female *T. tabaci* demonstrated a significant preference for *A. fistulosum* over the cv. Alibaba throughout the test period and cv. Bila throughout the test period except for the first 10 minutes (Figure 2 f, h). When common onion cultivars Alibaba and Bila were paired with cv. Tęcza, the settling preference of *T. tabaci* females was different. A

significantly higher number of thrips settled on cv. Alibaba compared to cv. Tęcza, whereas cv. Tęcza was preferred over Bila (Figure 2 e, g). For the pairs Alibaba x Bila (Figure 2 b) and Tęcza x Kroll (Figure 2 a) there were no significant differences in onion thrips' preference.

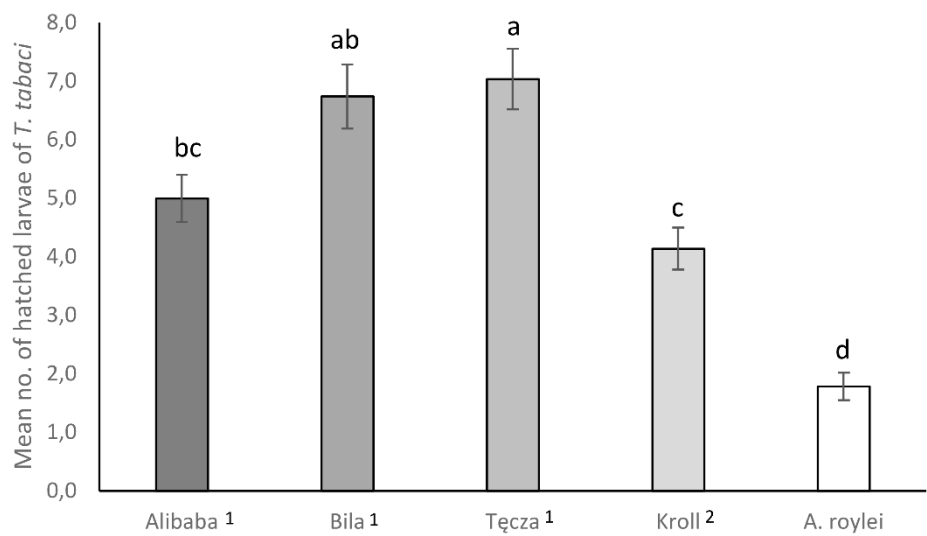
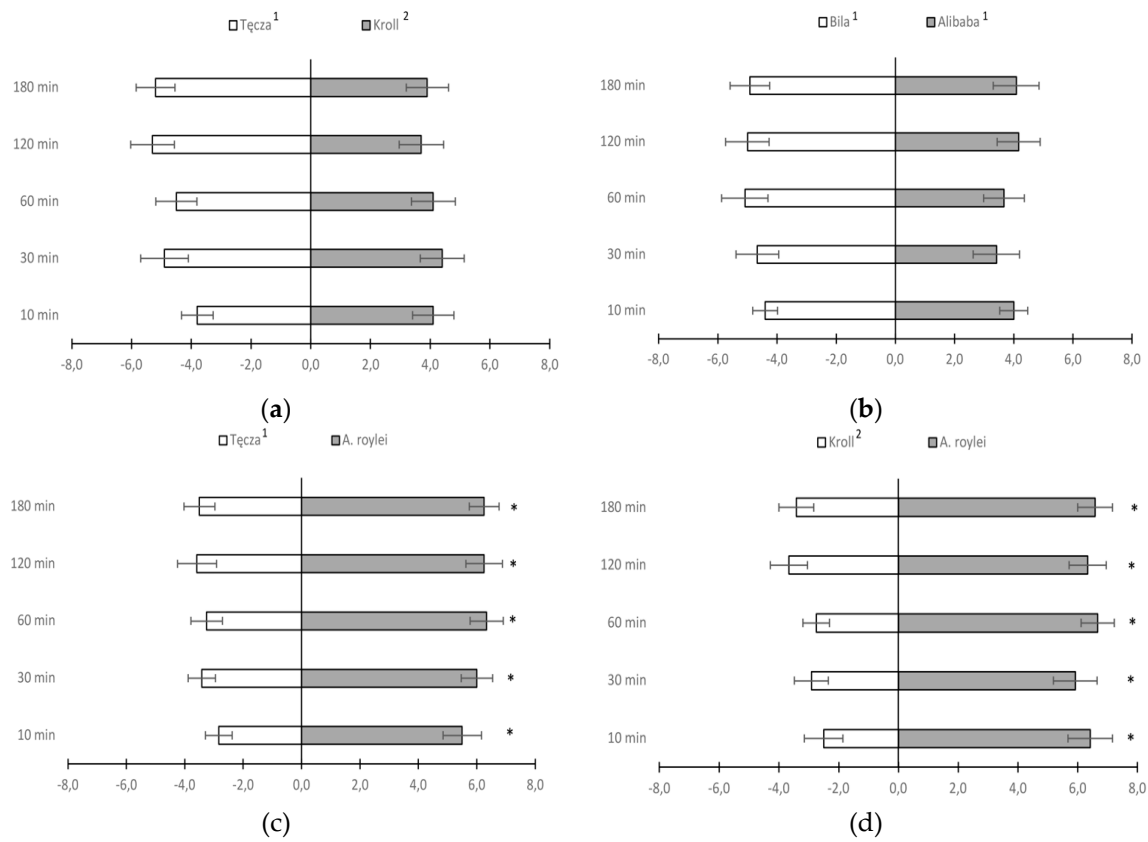


Figure 1. Mean (\pm SE) number of hatched larvae of *Thrips tabaci* on cvs. Tęcza¹, Alibaba¹, Bila¹, Kroll² and *Allium roylei*. ¹*Allium cepa*, ²*A. fistulosum*. Means with the same letters on each bar do not differ significantly (Tukey HSD test, $p < 0.05$).



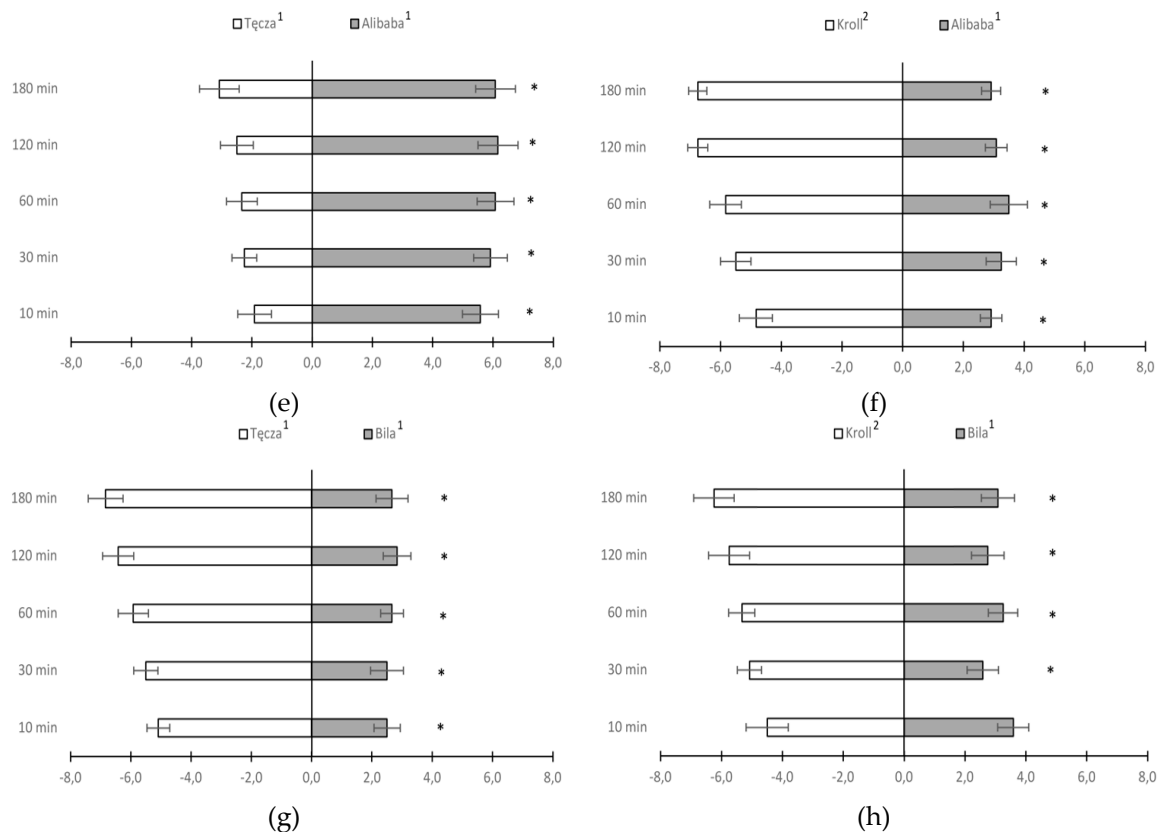


Figure 2. Mean number (\pm SE) of *Thrips tabaci* females settled on leaf sections from two compared onion cultivars/species 10 min, 30 min and 1, 2, and 3 h after their release (* bars showing the significant difference in thrips settlement on the compared onion cultivars - Student t test at p < 0.05); ¹*Allium cepa*, ²*A. fistulosum*.

4. Discussion

Our experiments were short-term laboratory experiments that only provide information on thrips' selection behavior at the first stage of colonization and acceptance of the plant for egg-laying. The observed differences in the numbers of hatched larvae indeed reflect differences in oviposition (numbers of eggs from which the larvae have hatched). Among the three onion species tested (*A. cepa*, *A. fistulosum*, and *A. roylei*), the most frequently colonized by *T. tabaci* females was *A. roylei*. While adult *T. tabaci* did not respond to *A. cepa* plant odor in a Y-tube olfactometer [14], plant volatiles from *A. roylei* leaf sections may have attracted *T. tabaci* during the 3 h period in this study. Olfactometer tests using *T. tabaci* and *A. roylei* plants could help to clarify this possible attraction. On the contrary, in the oviposition bioassay without choice over a 24-hour period, four times fewer larvae hatched on the leaves of *A. roylei* than on the common onion cv. Tęcza and almost two times fewer than on Welsh onion. It has been hypothesized by some authors that thrips and other herbivores females would prefer those leaves for oviposition on which they realize the highest reproductive success [35-37]. Lower fecundity of females on leaves of *A. roylei* could therefore result from less favorable conditions for feeding and development of offspring. In our earlier field studies we noticed that despite the presence of *T. tabaci* on the leaves of *A. roylei*, no damage caused by thrips feeding on them was observed, in contrast to the injured leaves of *A. cepa* and *A. fistulosum* [33]. The lower oviposition rate of females on *A. roylei* leaves under laboratory conditions and the lack of damage to the leaves under field conditions – when *T. tabaci* had a choice between many cultivars and the breeding lines of *A. cepa* and *A. fistulosum* – may suggest that this wild onion species has some traits of resistance to *T. tabaci* which discourage thrips from feeding and egg laying. *A. roylei* is a plant with narrow, drooping leaves which are sometimes described as filiform. Mature, full-sized leaves are fistulous, though smaller ones are sometimes solid. In turn, *A. fistulosum* (cv. Kroll) leaves are wide, erect and pointed hollow tubes and are more similar to the cylindrical, fleshy, and hollow leaves of

A. cepa [38] (authors' observations). Differences between resistance to thrips of the tested onion species may be due to certain morphological features of their leaves, which make it difficult for females to lay eggs. They may concern the thickness and rigidity of the cellular wall, the amount of epicuticular waxes, the structure of the epidermis, and the number of stomates [39,40]. Post-alighting host acceptance, and also subsequent feeding and reproduction, are strongly influenced by the plant's nutritional quality and defenses such as secondary metabolites [41,42]. Many bioactive metabolites like cysteine, sulfoxides, flavanols, polyphenols, and saponins are synthesized by different organs of *A. roylei* to provide defense against a wide range of plant pathogens and herbivores [43,44]. Resistance against downy mildew (*Peronospora destructor* (Berk.) Casp. ex Berk.) was identified in *A. roylei* and successfully transferred to bulb onion [28]. This wild onion is partially resistant to leaf blight disease caused by *Botrytis squamosa* J. C. Walker and basal rot disease caused by *Fusarium oxysporum* f. sp. *cepae* [29,45]. Also, *A. roylei* has been proven to be partially resistant to beet armyworm *Spodoptera exigua* Hübner. Larval growth and survival of *S. exigua* proved to be significantly slower on *A. roylei* compared to the *A. cepa*, *A. fistulosum*, and *A. galanthum* Kar. et Kir. [46]. The prospect of using *A. roylei* as a source of resistance to *T. tabaci* in onion breeding is promising, but further research is needed on how many larvae can complete development, how quickly they will develop, and what will be the final condition and fertility of the next generation of females.

In our bioassay, *A. fistulosum* cv. Kroll was more frequently chosen for settling by female *T. tabaci* than the two cultivars of *A. cepa* i.e., Alibaba and Bila, but a significantly lower number of larvae hatched from eggs laid by females on leaves of *A. fistulosum* compared with leaves of two cultivars of *A. cepa*, i.e. Bila and Tęcza. In our field study, despite the very high number of thrips caught from the leaves of *A. fistulosum*, minor damage was recorded on them [33]. The leaves of *A. fistulosum* were damaged by feeding thrips only in 6.5% of cases in 2015 and 1.5% of cases in 2016 (unpubl. data) while the corresponding figures for leaves of *A. cepa* cvs. Alibaba, Bila, and Tęcza were, respectively, 13.5%, 13.9%, and 17.8% in 2015 and 5.3%, 6.8%, and 7.3% in 2016 [20]. This was also confirmed by a field study by Hudák and Péntzes [47], where *A. fistulosum* showed less damage than *A. cepa* under similar field conditions. It confirms that *T. tabaci* has shown higher affinity toward *A. fistulosum* phenotype during settlement and supports higher densities of thrips, but *A. cepa* creates better conditions for foraging and laying eggs. Ren et al. [48] proved that volatiles are important factors for thrips in host preference. In their study, one of the most attractive volatiles, along with *Medicago sativa*, for *T. tabaci* and *Frankliniella occidentalis* Pergande appeared to be volatiles of *A. fistulosum* in its vegetative and flowering stages. In turn, Jones et al. [49] showed that the Nebuka type of *A. fistulosum* has a similar low degree of thrips colonization as the resistant cv. White Persian of *A. cepa*. The authors noted that the leaves of both *Allium* sp. were circular, and they had a spreading growth habit and a long sheath region. Some authors report that *A. fistulosum* can be used for improvement of the common onion, especially for its resistance to pink root (*Phoma terrestris* E. M. Hans.) [50], Fusarium basal rot, *T. tabaci*, smut (*Urocystis cepulae* Frost) [51], and onion fly (*Hylemya antiqua* Bouche) [52]. Varietal resistance against *Liriomyza chinensis* (Kato) has been reported in *A. fistulosum* in Japan. Antibiosis studies revealed a significant difference in survival up to the pupal stage, in the forewing lengths of adults and in the development time from the egg to pupal stages among the resistant and susceptible varieties of *A. fistulosum* [53,54]. *A. fistulosum*, as well as wild *Allium* species like *A. hookeri*, *A. altaicum*, and *A. angulosum*, are a rich source of lectins and these compounds have recently been proven to have insecticidal activity against *T. tabaci* [55]. The authors suggest that the high lectin content of *A. hookeri* and *A. fistulosum* can be correlated with the low amount of thrips damage. Whole plant and detached leaf damage tests revealed that *A. hookeri* was resistant to *T. tabaci*. However, worse development of this pest was observed not only on *A. hookeri*, but also on *A. fistulosum*. There are many local and commercial cultivars of *A. fistulosum* with distinctive differences in morphological and other traits which are adapted to a variety of climatic conditions. The wide variety of *A. fistulosum* phenotypes that exists around the world [56] suggests that some of them will likely develop traits that will promote resistance or tolerance to *T. tabaci*, so further research in this direction appears to be justified.

In a previous field study, cv. Tęcza was resistant to thrips abundance but susceptible to thrips feeding and was more heavily damaged than varieties susceptible to thrips infestation and foraging cv. Alibaba [20]. Although the laboratory test did not show significant differences in the number of hatched *T. tabaci* larvae between tested cultivars of *A. cepa*, the highest number of them was recorded on cv. Tęcza. Perhaps the cv. Tęcza, which stimulated *T. tabaci* individuals to feed more under field conditions, could also stimulate females to lay eggs more intensively during the bioassay test. In the settlement test in the Alibaba x Tęcza pairing, the most preference was exhibited by female onion thrips to the cv. Alibaba, but in pair of Bila x Tęcza, cv. Tęcza was preferred to cv. Bila. In a field study, Alibaba was also more populated by *T. tabaci* than cv. Tęcza but cv. Tęcza appeared to be less attractive than cv. Bila [20]. Laboratory tests do not always reflect the behavior of insects in the field, where they are influenced by many abiotic and biotic factors, and the results obtained must be interpreted with this in mind.

5. Conclusions

The choice between *A. cepa*, *A. roylei* and *A. fistulosum* by the females of *T. tabaci* in the tests on the preference for settlement and the rate of oviposition was the opposite. This confirms results obtained by other researchers that other plants' characteristics attract females to colonize them, and others stimulate them to lay eggs [57]. Since the lowest number of larvae hatched on *A. roylei*, followed by *A. fistulosum*, it can be assumed that the leaves of these species have certain traits that discourage or inhibit females from laying eggs or hatching larvae. For this reason, these species should be studied in the future for the biology of *T. tabaci* on them and for the features, both morphological, anatomical, and biochemical, that may impede the development of thrips.

Author Contributions: For research articles with several authors, a short paragraph specifying their individual contributions must be provided. The following statements should be used "Conceptualization, M.O. and M.P.; methodology, E.K. and M.O.; software, M.P. and T.W.; validation, M.P. and M.O.; formal analysis, M.P.; investigation, M.O. and E.K.; resources, M.P. and T.W.; data curation, M.O. and M.P.; writing—M.P. and M.O.; writing—review and editing, M.P.; M.O. and E.K.; visualization, T.W. and M.P.; supervision, M.P. and M.O.; project administration, M.P. and E.K.; funding acquisition M.P. and E.K. All authors have read and agreed to the published version of the manuscript." Please turn to the [CRediT taxonomy](#) for the term explanation. Authorship must be limited to those who have contributed substantially to the work reported.

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Institutional Review Board Statement: All animal work was conducted according to relevant national and international guidelines. For insect collection, no permits were required since the area where thrips were collected did not contain any strictly protected areas, and *Thrips tabaci* is not under protection in Europe. Also, no permits were required to use insects for experiments due to the observational nature of the data collection.

Data Availability Statement: The data presented in this study are openly available in Harvard Dataverse: <https://doi.org/10.7910/DVN/5KCCM7> accessed date 16 July 2023.

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