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The Preference of *Thrips tabaci* for *Allium cepa*, *Allium fistulosum*, and *Allium roylei*

Marta Olczyk [1], Elisabeth H. Koschier [2], Tomasz Wójtowicz [3] and Maria Pobożniak [1,*]

[1] Department of Botany, Physiology and Plant Protection, Faculty of Biotechnology and Horticulture, University of Agriculture in Krakow, 31-425 Krakow, Poland; marta.olczyk@urk.edu.pl
[2] Institute of Plant Protection, Department of Crop Sciences, University of Natural Resources and Life Sciences (BOKU), Gregor Mendel-Strasse 33, 1180 Vienna, Austria; elisabeth.koschier@boku.ac.at
[3] Department of Plant Breeding, Physiology and Seed Science, Faculty of Agriculture and Economics, University of Agriculture in Krakow, 31-120 Krakow, Poland; tomasz.wojtowicz@urk.edu.pl
* Correspondence: maria.pobozniak@urk.edu.pl

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. Today, the Integrated System of Production and Plant Protection requires onion growers to use onion- thrips-resistant cultivars. It has become apparent that the improvement of existing onion cultivars may not be a sufficient, so it is necessary to search 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 the 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 the leaves of cv. Alibaba. Statistically significant differences between cultivars/species were found in the number of hatched larvae on the leaves of the tested cultivars/species of onion. The lowest number of larvae hatched from eggs laid on *A. roylei*, as compared to *A. fistulosum* and the cultivars of *A. cepa*, except for Bila.

Keywords: bioassay; oviposition; settling preference; resistance

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1. Introduction

Onion (common onion or bulb onion) (*Allium cepa* L.) is a universal vegetable popular in many cuisines around the world, with a global total production of 93,226,400 tonnes, and it accounts for approximately 24% of the world's total vegetable production [1]. Onion production and breeding involve 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 a vector of several onion pathogens and tospoviruses [4–8]. An attack by *T. tabaci* not only leads to a complete loss of onion seedlings but may also cause damage to older crops due to the pest's feeding on leaves as well as onion bulbs [9]. The low effectiveness of insecticides in controlling thrips—and thrips' increased resistance to them—leads to high losses in the cultivation of onions [10,11]. A reduction in yields of approximately 40–65% has been reported due to attacks by these pests [12,13]. The full resistance (or tolerance) of onion to *T*. *tabaci* would be highly 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], the 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 onion genotypes that showed a lower number of thrips compared to susceptible ones [19,21], and these produced large bulb yields under thrips pressure [17,22].

Onion breeding programs currently focus mainly on the improvement of existing cultivars; however, many desirable traits, such as resistance to diseases and pests, are possessed by wild Allium species [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 characteristics that are 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 was conducted under laboratory conditions 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 the 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 registered 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 Nochowo (cv. Tęcza). *A. roylei* seeds we obtained from the bank of 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 ± 1 °C in 35 ± 5% relative humidity, with a photoperiod of 16:8 h of light/dark. All plants were watered regularly with tap water alone. Leaves from onion plants that were approximately four weeks old were used in all the bioassays.

2.2. Test Insects

Using a rearing method adapted from Loomans and Murai [34], a stock culture of a thelytokous *T. tabaci* strain was maintained on white cabbage leaves in 0·75 L glass jars covered with a fine mesh to ensure ventilation. The rearing was conducted in a climate chamber at 24 ± 1 °C in 35 ± 5% relative humidity, with a photoperiod of 16:8 h of 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 for air circulation and were sealed with a sealing film to prevent the thrips from escaping. After 48 h, the adult females were checked, and any remaining pupae were removed. Following an additional pre-oviposition period of 48 h, 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 a thin (14 μm), clear plastic film (Carl Roth, Karlsruhe, Germany), which was perforated (one hole per cm^2 on average) using insect pins (0·4 mm diameter). The bioassay units were kept in a climate chamber at 24 ± 1 °C in $35 \pm 5\%$ relative humidity, with a photoperiod of 16:8 h of light/dark. After 24 h, 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 a perforated plastic film and completely randomized under an artificial light source in a climate chamber at 24 ± 1 °C and in $35 \pm 5\%$ relative humidity. Then, 10, 30, 60, 120, and 180 min 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., Palo Alto, CA, USA, 2017). The results of the settling preference tests were analyzed with Student's *t*-test for an unequal sample size (12 replications, with only 10 replications for Tęcza × Kroll) with a significance level of $p < 0.05$. The normality of the distribution of the tested samples was checked with the Shapiro–Wilk test, and log(x + 1) transformation was performed in the case of a lack of normality. The data obtained from the oviposition tests with the hatched thrips larvae were subjected to a one-way analysis of variance (ANOVA), with the factor of the onion cultivar/species and an unequal number of replications (cv. Tęcza = 26, cv. Alibaba = 28, cv. Bila = 27, cv. Kroll 43, sp. *A. roylei* = 37). Residual plots were checked prior to data analysis. In cases where the data did not show a normal distribution, they were normalized through log(x + 1) transformation. The Tukey test for an unequal sample size was used to compare the 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 the 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 the 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).

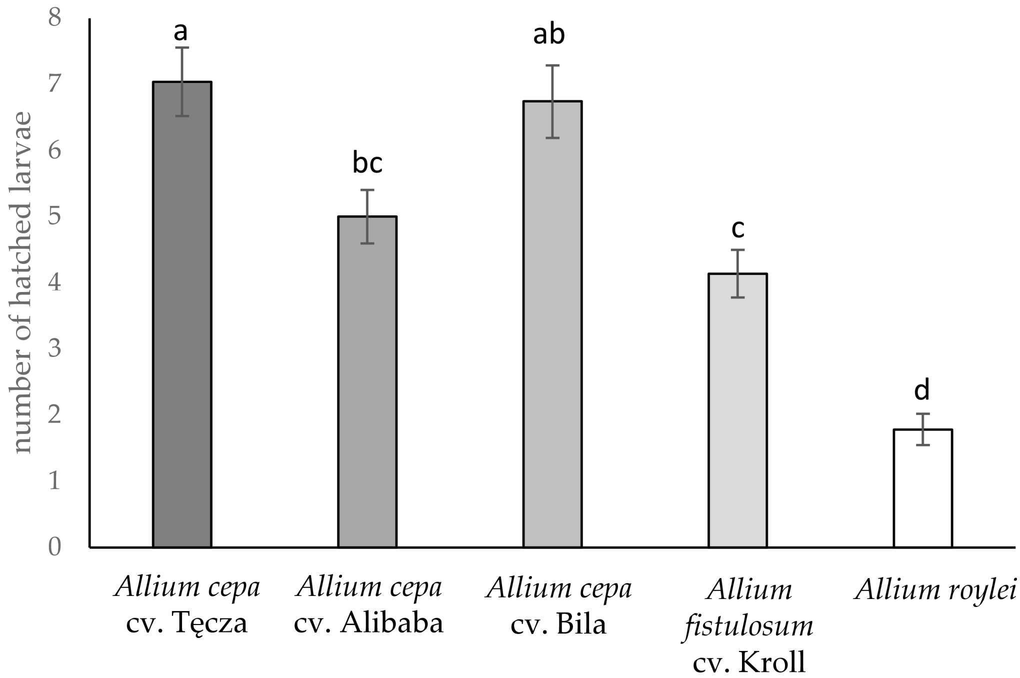

Figure 1. Mean (±SE) number of hatched larvae of *Thrips tabaci* on cvs. Tęcza [1], Alibaba [1], Bila [1], Kroll [2], and *Allium roylei.* [1] *Allium cepa*, [2] *A. fistulosum*. Sample size: Alibaba *n* = 28, Bila *n* = 27, Tęcza *n* = 26, Kroll *n* = 43, *A. roylei n* = 37. Means with the same letters on each bar do not differ significantly (Tukey's HSD test, $p < 0.05$).

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 the 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 the leaf sections of *A. roylei*. When the *A. cepa* cultivars were paired with cv. Kroll (*A. fistulosum*), the female *T. tabaci* demonstrated a significant preference for *A. fistulosum* over cv. Alibaba and cv. Bila throughout the test period, except for the first 10 min (Figure 2f,h). When the 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 2e,g). For the pairs Alibaba × Bila (Figure 2b) and Tęcza × Kroll (Figure 2a), there were no significant differences in the onion thrips' preference.

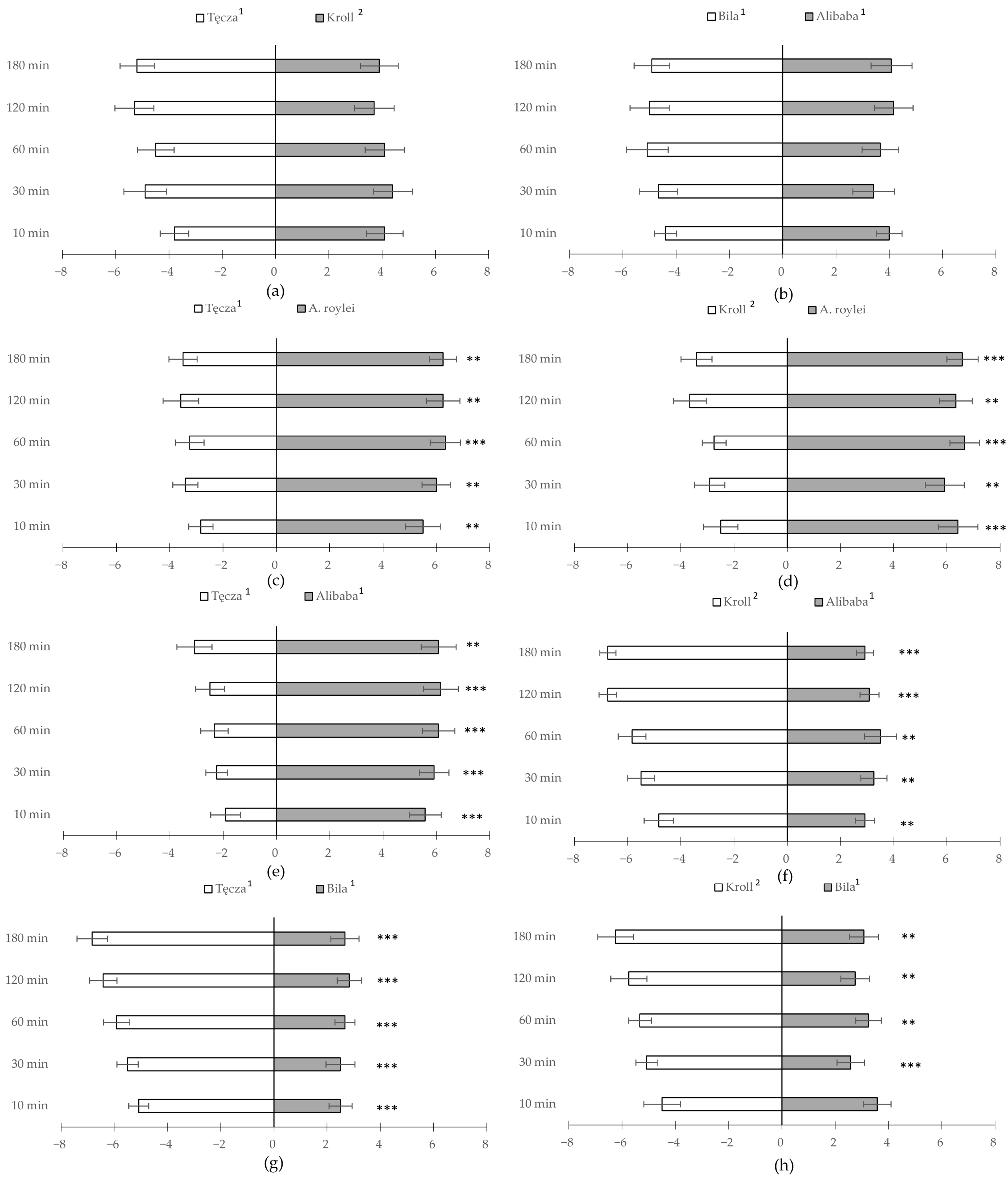

Figure 2. Mean number (±SE) of *Thrips tabaci* females settled on leaf sections from the two compared onion cultivars/species 10, 30, 60, 120, and 180 min after their release (**/*** bars showing the significant difference in thrips settlement on the compared onion cultivars—Student's *t*-test at $p < 0.01/0.001$); [1] *Allium cepa*, [2] *A. fistulosum*. (**a**) Tęcza × Kroll; (**b**) Bila × Alibaba; (**c**) Tęcza × *A. roylei*; (**d**) Kroll × *A. roylei*; (**e**) Tęcza × Alibaba; (**f**) Kroll × Alibaba; (**g**) Tęcza × Bila; (**h**) Kroll × Bila. Number of repetitions: 12, with only 10 for Tęcza × Kroll.

4. Discussion

Our experiments were short-term laboratory experiments that only provided information on the thrips' selection behavior in 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 (the number of eggs from which the larvae 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 the adult *T. tabaci* did not respond to the *A. cepa* plant's odor in a Y-tube olfactometer [14], plant volatiles from the *A. roylei* leaf sections may have attracted *T. tabaci* during the 180 min 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 h period, four times fewer larvae hatched on the leaves of *A. roylei* than on the common onion cv. Tęcza, this being almost two times fewer than on the Welsh onion. It has been hypothesized by some authors that thrips and other herbivore females would prefer those leaves for oviposition that create the best conditions for the development of offspring and thus achieving the greatest reproductive success [35–37]. The lower fecundity of females on the leaves of *A. roylei* could therefore result from less favorable conditions for the 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 the 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 the *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 in resistance to thrips between 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 [18,39,40]. Onion genotypes (*A. cepa*) with less epidermal wax on their leaves are less frequently attacked and less susceptible to *T. tabaci* feeding. The large amounts of cuticle wax on most onion cultivars available in cultivation allow thrips to adhere to the leaf surface and cause damage [15]. Onion genotypes resistant or moderately resistant to *T. tabaci* have densely arranged wax crystals in the form of filaments, rods, and tubes [15,16]. Onions with more epidermal wax on their leaves tend to have darker leaves than those with less wax, which are usually lighter in color [15,41,42]. In research conducted by Diaz-Montano et al. [14], two cvs. Yankee and Nebula had blue-green foliage and were colonized by higher thrips populations, whereas 15 cultivars with yellow-green-colored leaves had a significantly lower number of thrips. Other authors indicated that the resistance of onion genotypes to thrips is also influenced by the structure of the plant, because this pest feeds mainly in the axils of the basal parts of the leaves. The narrower axils of onion leaves prevent thrips from accessing them, making them more resistant [17,18].

Post-alighting host acceptance and subsequent feeding and reproduction are strongly influenced by the plant's nutritional quality and defenses such as secondary metabolites [43,44]. A negative relationship between the total phenol content and thrips damage was observed by researchers studying the biochemical basis of onions' resistance to *T. tabaci* [19,20]. Njau et al. [19] and Bhonde et al. [45] found that the total sugar content in the leaves of onion genotypes was positively correlated with the number of onion thrips, while Pobożniak et al. [20] confirmed the positive correlation between reducing sugar quantity and thrips density.

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 [46,47]. Resistance against downy mildew (*Perenospora 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. *cepa* [29,48]. Also, *A. roylei* has been proven to be partially resistant to beet armyworm *Spodoptera exigua* Hübner. The larval growth and survival of *S. exigua* proved to be significantly slower on *A. roylei* compared to *A. cepa, A. fistulosum*, and *A. galanthum* Kar. et Kir. [49]. The prospect of using *A. roylei* as a source of resistance to *T. tabaci* in onion breeding is promising, but further research is needed to determine how many larvae can complete their development, how quickly they will develop, and what the final condition and fertility of the next generation of females will be.

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 the 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 in a field study conducted by Hudák and Pénzes [50], where *A. fistulosum* showed less damage than *A. cepa* under similar field conditions. This confirms that *T. tabaci* has a higher affinity toward the *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. [51] proved that volatiles are important factors for thrips in regard to 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 the volatiles of *A. fistulosum* in its vegetative and flowering stages. In turn, Jones et al. [52] 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 the improvement of the common onion, especially for its resistance to the pink root (*Phomaterrestris* E. M. Hans.) [53], Fusarium basal rot, *T. tabaci*, smut (*Urocystisce pulae* Frost) [54], and onion fly (*Hylemya antiqua* Bouche) [54]. Varietal resistance against *Liriomyza chinensis* (Kato) has been reported in *A. fistulosum* in Japan. Antibiosis studies have shown significant differences 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* [55,56]. *A. fistulosum* and 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* [57]. 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, an inferior 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 that are adapted to a variety of climatic conditions. The wide variety of *A. fistulosum* phenotypes that exist around the world [58] suggests that some of them will likely develop traits that will promote resistance or tolerance to *T. tabaci*; thus, 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 the tested cultivars of *A. cepa*, the highest number of larvae 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 × Tęcza pairing, the greatest preference exhibited by female onion thrips was that for cv. Alibaba, but in the pairing Bila × 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* exhibited by the females of *T. tabaci* was the opposite in the tests on the preference for settlement and on the rate of oviposition. This may indicate that other plants' characteristics attract females to colonize them, and others stimulate them to lay eggs. 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* and for the features, including the morphological, anatomical, and biochemical, that may impede the development of thrips.

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Institutional Review Board Statement: All animal work was conducted according to the relevant national and international guidelines. For insect collection, no permits were required since the area where the 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 the experiments due to the observational nature of the data collection.

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

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