



Uniwersytet Rolniczy im. H. Kołłątaja w Krakowie
Wydział Biotechnologii i Ogrodnictwa

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**Skład gatunkowy, występowanie, żerowanie
i szkodliwość wciornastków na cebuli**

Praca doktorska

Praca wykonana pod kierunkiem
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Tytuł pracy w języku
polskim

Skład gatunkowy, występowanie, żerowanie i szkodliwość wciornastków na cebuli

Słowa kluczowe
/ maksymalnie 5 słów /

odporność, barwa, cukry, fenole, epiderma

Streszczenie pracy
/ maksymalnie 1200 znaków /

W latach 2014-2016 na *Allium cepa* i *A. fistulosum* stwierdzono 9 gatunków wciornastków. Najliczniejszym na *A. cepa* był *Thrips tabaci* (64,4%) a na *A. fistulosum* *Frankliniella intonsa* (62,7%). Liczny był także *Aeolothrips intermedius*. Proporcje między nimi zmieniły się w ciągu sezonu wegetacyjnego. Analiza barwy liści 8 odmian *A. cepa* w latach 2015-2016 wykazała, że 'Tęcza' i 'Wenta' o ciemniejszych, zielono-szaro-żółtawych liściach były mniej atrakcyjne dla migrujących osobników *T. tabaci*. W latach 2015-2016 uznano, że 'Wenta' była odporna na rozwój i żerowanie *T. tabaci*, a 'Tęcza' na jego rozwój. Wykazano dodatnią korelację między stężeniem cukrów redukujących a liczebnością wciornastków. W obu latach stwierdzono ujemną zależność między całkowitą zawartością fenoli a uszkodzeniami powodowanymi przez wciornastki. Cieńsza warstwa epidermy, mniejsza powierzchnia komórek epidermalnych i mezofilnych oraz mniejsza średnica wiązek naczyniowych mogą sprzyjać odporności odmian cebuli na wciornastki. Żerowanie wciornastków spowodowało obniżenie zawartości cukrów rozpuszczalnych, sacharozy i barwników roślinnych w liściach odmian *A. cepa* zaś zwiększenie zawartości fenoli.

Tytuł pracy w języku
angielskim

The species composition, occurrence, feeding and harmfulness of thrips on onion

Słowa kluczowe
/ maksymalnie 5 słów /

resistance, colour, sugars, phenols, epiderma

Streszczenie pracy
/ maksymalnie 1200 znaków /

In 2014-2016, 9 thrips species were found on *Allium cepa* and *A. fistulosum*. The most numerous on *A. cepa* was *Thrips tabaci* (64.4%) and on *A. fistulosum* *Frankliniella intonsa* (62.7%). *Aeolothrips intermedius* was also abundant. The proportions between them varied during the growing season. Leaf colour analysis of 8 *A. cepa* cultivars in 2015-2016 found that 'Tęcza' and 'Wenta' with darker, green-grey-yellowish leaves were less attractive to migrating individuals of *T. tabaci*. In 2015-2016, 'Wenta' was found to be resistant to the development and feeding of *T. tabaci*, while 'Tęcza' was resistant to its development. A positive correlation was found between the concentration of reducing sugars and thrips abundance. In both years, a negative correlation was found between total phenolic content and damage caused by thrips. A thinner epidermal layer, a smaller epidermal and mesophyll cell area and a smaller vascular bundle diameter may promote thrips resistance in onion cultivars. Thrips feeding caused a decrease in soluble sugars, sucrose and plant pigments in the leaves of *A. cepa* cultivars, while increasing the phenolic content.

Maria Pobożniak

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Pracę doktorską realizowałam w Katedrze Botaniki, Fizjologii i Ochrony Roślin (KBFiOR) w latach 2013-2022 w ramach studiów doktoranckich prowadzonych w Studium Doktoranckim Uniwersytetu Rolniczego im. Hugona Kołłątaja w Krakowie.

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Córcie Łucji za to, że rozumiała i była blisko,

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1. Wykaz publikacji

1.1. Cykl publikacji będący przedmiotem rozprawy doktorskiej

Przedstawiony do oceny cykl publikacji powiązanych tematycznie składał się z trzech artykułów naukowych:

1. **Olczyk, M.**, Pobożniak, M. (2020). Thrips (Thysanoptera) associated with onion (*Allium cepa* L.) and Welsh onion (*Allium fistulosum* L.). *Folia Horticulturae*, 32(2), 319-335, <https://doi.org/10.2478/fhort-2020-0028>.

Punktacja MNiSW₂₀₂₀: **20**

IF₂₀₂₀: **1,873**

2. Pobożniak, M., **Olczyk, M.**, Wójtowicz T. (2021). Relationship between colonization by onion thrips (*Thrips tabaci* Lind.) and leaf colour measures across eight onion cultivars (*Allium cepa* L.). *Agronomy*, 11(5), 963, <https://doi.org/10.3390/agronomy11050963>.

Punktacja MNiSW₂₀₂₁: **100**

IF₂₀₂₁: **3,417**

3. Pobożniak, M., **Olczyk, M.**, Wójtowicz, T., Kamińska, I., Hanus-Fajerska, E., Kostecka-Gugała, A., Kruczek, M. (2022). Anatomical and biochemical traits associated with field resistance of onion cultivars to onion thrips and the effect of mechanical injury on the level of biochemical compounds in onion leaves. *Agronomy*, 12(1), 147, <https://doi.org/10.3390/agronomy12010147>.

Punktacja MNiSW₂₀₂₂: **100**

IF₂₀₂₂: **3,417**

Sumaryczna punktacja MNiSW: 220

Sumaryczny IF: 8,707

Publikacje będące przedmiotem rozprawy doktorskiej zawierają osobny wstęp, opis materiałów i metod badawczych, wyniki, dyskusję oraz podsumowanie i wnioski. Z tego względu w niniejszym autoreferacie zostały omówione najważniejsze wyniki badań dla każdej z publikacji. Podsumowanie oraz wnioski końcowe zostały przedstawione łącznie dla wszystkich trzech publikacji.

1.2. Pozostałe prace

Artykuły naukowe:

1. Pobożniak, M., **Leśniak, M.** (2015). Application strategy for the chemical control of pea (*Pisum sativum* L.) crops against *Thrips tabaci* Lindeman, 1889 (Thysanoptera). *Polish Journal of Entomology*, 84(3), 177, <https://doi.org/10.1515/pjen-2015-0015>.
2. Pobożniak, M., **Leśniak, M.**, Chuda, A., Adamus, A. (2016). Field assessment of the susceptibility of onion cultivars to thrips attack – preliminary results. *Polish Journal of Entomology*, 85(1), 121, <https://doi.org/10.1515/pjen-2016-0006>.
3. Pobożniak, M., Grabowska, D., **Olczyk, M.** (2016). Effect of orange and cinnamon oil on the occurrence and harmfulness of *Thrips tabaci* Lind on onion – preliminary results. *Acta Horticulturae et Regiotecturae*, 19(s1), 13-14, <https://doi.org/10.1515/ahr-2016-0016>.

Czynny udział konferencyjny:

1. III International Conference of PhD Students ‘Multidirectional Research in Agriculture and Forestry’ University of Agriculture in Krakow, 22 March 2014. (Dyplom za zajęcie I miejsca w sesji referatowej „Ogrodnictwo i zielarstwo”).
2. 4th Symposium on Palaearctic Thysanoptera, Vienna, Austria 8th-11th September 2014.
3. 5th Symposium on Palaearctic Thysanoptera, Krakow, Poland 26th-29th September 2017.
4. 6th Symposium on Palaearctic Thysanoptera, Zamárdi, Hungary, 13th-17th September 2021.

Artykuły pokonferencyjne:

1. **Leśniak, M.**, Pobożniak, M., Pniak, M. (2014). The influence of orange oil and orange synthetic aroma on *Tetranychus urticae* (Koch.), *Aphis phomi* (Deg.) and *Eriosoma lanigerum* (Hasm.). *Episteme*, 22, 101-107. ISSN 1895-4421.
2. Grabowska, D., **Olczyk, M.**, Woszczyk, K., Pobożniak, M. (2016). Wstępne badania nad występowaniem wciornastków (Thysanoptera) na koprze ogrodowym *Anethum graveolens* L. *Episteme*, 30(2), 237-244. ISSN 1895-4421.
3. Grabowska, D., **Olczyk, M.**, Woszczyk, K., Pobożniak, M. (2016). Wstępne badania nad występowaniem wciornastków (Thysanoptera) na wybranych gatunkach czosnku *Allium* spp. *Episteme*, 30(2), 227-235. ISSN 1895-4421.

Referaty wygłoszone na konferencjach:

1. **Olczyk, M.,** Pobożniak, M. An overview of the thrips species found in the ‘Góra Bucze’ landscape-nature complex in Górkki Wielkie. 5th Symposium on Palaearctic Thysanoptera, Krakow, Poland 26th-29th September 2017.

Postery:

1. **Leśniak, M.,** Pobożniak, M., Chuda, A., Adamus, A. (2014). Field assessment of the susceptibility of onion to thrips – preliminary results. 4th Symposium on Palaearctic Thysanoptera, Vienna, Austria 8th-11th September 2014.
2. Grabowska, D., **Olczyk, M.,** Woszczyk, K., Pobożniak, M. (2016). Preliminary research on the occurrence of thrips (Thysanoptera) on dill *Anethum graveolens* L. 5th International Conference for Young Researchers ‘Multidirectional Research in Agriculture, Forestry and Technology’ University of Agriculture in Krakow, 16-17.04.2016.
3. **Olczyk, M.,** Koschier, E.H., Pobożniak, M. (2021). Preference of *Thrips tabaci* Lind. to *Allium cepa* L., *Allium fistulosum* L. and *Allium roylei* Stearn. 6th Symposium on Palaearctic Thysanoptera, Zamárdi, Hungary, 13th-17th September 2021.
4. Pobożniak, M., **Olczyk, M.,** Wójtowicz, T. (2021). Leaf colour can be a factor for varietal preference of onion thrips (*Thrips tabaci* Lind.) among eight onion varieties (*Allium cepa* L.). 6th Symposium on Palaearctic Thysanoptera, Zamárdi, Hungary, 13th-17th September 2021.

Doniesienie konferencyjne

1. **Leśniak, M.,** Pobożniak, M., Pniak, M. The influence of orange oil and orange synthetic aroma on *Tetranychus urticae* (Koch.), *Aphis phomi* (Deg.) and *Eriosoma lanigerum* (Hasm.). III International Conference of PhD Students ‘Multidirectional Research in Agriculture and Forestry’ University of Agriculture in Krakow, 22 March 2014.
2. **Leśniak, M.,** Pobożniak, M., Chuda, A., Adamus, A. Field assessment of the susceptibility of onion to thrips – preliminary results. 4th Symposium on Palaearctic Thysanoptera, Vienna, Austria 8th-11th September 2014.
3. Grabowska, D., **Olczyk, M.,** Woszczyk, K., Pobożniak, M. Preliminary research on the occurrence of thrips (Thysanoptera) on dill *Anethum graveolens* L. 5th International Conference For Young Researchers ‘Multidirectional Research in Agriculture, Forestry and Technology’ University of Agriculture in Krakow, 16-17.04.2016.

4. Grabowska, D., **Olczyk, M.**, Woszczyk, K., Pobożniak, M. Preliminary research on the occurrence of thrips (Thysanoptera) on garlic *Allium* spp. 5th International Conference For Young Researchers 'Multidirectional Research in Agriculture, Forestry and Technology' University of Agriculture in Krakow, 16-17.04.2016.
5. **Olczyk, M.**, Grabowska, D., Pobożniak, M. An overview of the thrips species found in the 'Góra Bucze' landscape-nature complex in Górki Wielkie. 5th Symposium on Palaearctic Thysanoptera, Krakow, Poland 26th-29th September 2017.
6. Pobożniak, M., **Olczyk, M.**, Wójtowicz, T. Leaf colour can be a factor for varietal preference of onion thrips (*Thrips tabaci* Lind.) among eight onion varieties (*Allium cepa* L.). 6th Symposium on Palaearctic Thysanoptera, Zamárdi, Hungary, 13th-17th September 2021.

Szkolenia i kursy krajowe

1. Szkolenie 'Praktyczna nauka identyfikacji wciornastków (Thysanoptera)'. Szkolenie zrealizowane w dniach 22-25.05.2017. Zakład Zoologii, Instytut Biologii i Biochemii, Wydział Biologii i Biotechnologii, Uniwersytet Marii Curie-Skłodowskiej w Lublinie.
2. Kurs 'Introduction to Acarology'. Kurs prowadzony przez Prof. dr Sebahat K. Ozman-Sullivan (Ondokuz Mayis University Samsun, Turkey) w dniach 23.04-17.06.2015. Wydział Biotechnologii i Ogrodnictwa, Uniwersytet Rolniczy im. Hugona Kołłątaja w Krakowie.
3. Kurs 'Applied Acarology'. Kurs prowadzony przez Prof. dr Sebahat K. Ozman-Sullivan (Ondokuz Mayis University Samsun, Turkey) w dniach 23.04-17.06.2015. Wydział Biotechnologii i Ogrodnictwa, Uniwersytet Rolniczy im. Hugona Kołłątaja w Krakowie.

Staż zagraniczny

1. Staż zagraniczny w ramach programu **ERASMUS +** realizowany w laboratorium Division of Plant Protection, Department of Crop Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Gregor-Mendel-Strasse 33, 1180 Vienna, Austria, pod kierunkiem Prof. dr Elisabeth Koschier w dniach 21.10.-20.12.2019.

2. Streszczenie

Celem badań było określenie składu gatunkowego, liczebności, stosunku płci oraz sezonowej dynamiki występowania wciornastków (Thysanoptera) na ośmiu odmianach cebuli zwyczajnej *Allium cepa* L. i jednej odmianie cebuli siedmiolatki *Allium fistulosum* L., ocena stopnia zasiedlenia, rozwoju i szkodliwości wciornastka tytoniowca (*Thrips tabaci* Lind.) na odmianach cebuli zwyczajnej, a także wyjaśnienie niektórych morfologicznych, anatomicznych i biochemicznych podstaw zasiedlania i żerowania wciornastków na tej roślinie. Realizacja badań pozwoliła na wytypowanie do uprawy odmian cebuli, które są najslabiej zasiedlane na początku i w całym okresie wegetacji, i na których wciornastek tytoniowiec najslabiej się rozwija i powoduje najmniejsze szkody, oraz na poznanie czynników zwiększonej podatności niektórych odmian cebuli na żerowanie, zasiedlenie i rozwój wciornastka tytoniowca. Celem doświadczenia było również zbadanie w jaki sposób żerowanie wciornastka tytoniowca wpływa na zmianę zawartości wybranych składników biochemicznych roślin.

Doświadczenia polowe prowadzono w latach 2014-2016 w Stacji Doświadczalnej Katedry Ochrony Roślin Uniwersytetu Rolniczego w Krakowie, położonej w Mydlnikach (koło Krakowa). W badaniach wykorzystano 8 odmian cebuli zwyczajnej ('Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁', 'Polanowska', 'Tęcza' i 'Wenta') i jedną odmianę cebuli siedmiolatki ('Kroll'). Nasiona każdej odmiany zostały wysiane w czterech powtórzeniach na poletkach o wymiarach 3 m × 4m (12 m²).

Obserwacje entomologiczne nad składem gatunkowym, liczebnością, dynamiką populacji wciornastków oraz ich szkodliwością dla cebuli prowadzono w odstępach dwutygodniowych w 2014 roku i cotygodniowych w latach 2015-2016. Wciornastki odławiano z poletek za pomocą standardowego czerpaka entomologicznego oraz zbierano bezpośrednio z liści roślin. Następnie w warunkach laboratoryjnych wciornastki były preparowane i oznaczane. W pracy oszacowano stopień uszkodzenia liści cebuli spowodowanych przez żerujące wciornastki oraz oceniono wpływ uszkodzeń mechanicznych spowodowanych przez żerujące osobniki wciornastka tytoniowca na zawartość wybranych związków biochemicznych (cukrów rozpuszczalnych, redukujących i sacharozy, chlorofilu a i b oraz karotenoidów) w liściach cebuli. W celu poznania czynników wpływających na zasiedlenie, liczebność i żerowanie wciornastka tytoniowca oznaczono zawartość w liściach cukrów (rozpuszczalnych, redukujących i sacharozy), fenoli ogółem, a także zbadano niektóre cechy ich anatomicznej budowy. Wykonano również pomiar parametrów barwy liści cebuli za pomocą

spektrofotometru (Konica Minolta Chroma Meter CM-2600d) z uwzględnieniem przestrzeni barw CIELAB (CIE 1976 L*a*b*) i CIE L*C*h*.

W doświadczeniach przeprowadzonych w latach 2014-2015 stwierdzono, że na odmianach cebuli zwyczajnej najliczniejszym gatunkiem był wciornastek tytoniowiec, a następnie wciornastek kwiatowiec (*Frankliniella intonsa* Trybom), podczas gdy na cebuli siedmiolatce obserwowano odwrotną kolejność. Trzecim pod względem liczby zebranych osobników był drapieżny gatunek wciornastek pstrokacz (*Aeolothrips intermedius* Bagnall). Wykazano również, iż u trzech wymienionych najliczniejszych gatunków wciornastków populacje głównie tworzyły samice. Najbardziej zasiedloną przez wciornastki odmianą okazała się 'Kroll' cebuli siedmiolatki, natomiast odmiany cebuli zwyczajnej w kolejnych latach wykazywały różny stopień atrakcyjności dla wciornastków. Ponadto zaobserwowano, że występowanie trzech najbardziej licznych gatunków wciornastków zmieniało się podczas sezonu wegetacyjnego. W czerwcu z reguły najliczniejszy był wciornastek tytoniowiec, natomiast w lipcu wzrastał udział procentowy wciornastka kwiatowca oraz drapieżnego wciornastka pstrokacza.

Podczas 2-letnich badań w latach 2015-2016 stwierdzono, że barwa liści testowanych odmian cebuli zwyczajnej ma wpływ na ich kolonizację przez migrujące osobniki wciornastka tytoniowca we wczesnym okresie wegetacji. Stwierdzono, że większa wartość parametru jasności L*, współrzędnej b*, nasycenia barwy (C*), kąta barwy (h*) oraz mniejsza wartość współrzędnej (a*) były istotnie skorelowane z liczbą wciornastków. Stwierdzono, iż intensywnie żywe zielono-żółte zabarwienie liści odmian podatnych: 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁' i 'Polanowska' mogło być przyczyną zwiększonej ich atrakcyjności dla migrujących wciornastków. W pracy wytypowano dwie odmiany 'Tęcza' i 'Wenta' o ciemniejszych zielono-szaro-żółtawych liściach jako odporne (mało atrakcyjne) na zasiedlenie przez wciornastka tytoniowca w początkowym okresie ich kolonizacji.

W latach 2015-2016 stwierdzono, że odmiany cebuli zwyczajnej różnią się podatnością na zasiedlenie, rozwój oraz stopień uszkodzenia liści przez żerujące osobniki wciornastka tytoniowca. Uznano, że odmiana 'Wenta' była umiarkowanie odporna na rozwój wciornastka tytoniowca oraz odporna na jego żerowanie. Z kolei odporna na rozwój wciornastków odmiana 'Tęcza' była niestety podatna na żerowanie tych szkodników. Pozostałe sześć odmian 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁' i 'Polanowska' były podatne zarówno na rozwój, jak i żerowanie wciornastka tytoniowca, przy czym odmiana 'Niagara F₁' była wysoce podatna na rozwój, a odmiana 'Polanowska' na żerowanie wciornastków. Wszystkie podatne

odmiany cebuli zwyczajnej na rozwój i żerowanie wciornastków były również podatne na ich kolonizację przez migrujące dorosłe wciornastki we wczesnym okresie rozwoju roślin, przy czym najbardziej atrakcyjna była odmiana 'Niagara F₁'. Z kolei odmiana 'Tęcza' była odporna, a odmiana 'Wenta' była średnio odporna na zasiedlenie przez kolonizujące je wciornastki.

Wyniki badań wskazują że odporność niektórych odmian cebuli zwyczajnej na rozwój i żerowanie wciornastków może mieć związek z mechanizmem antyksenozы i/lub antybiozy, które z kolei mogą być związane z zawartością cukrów i fenoli w liściach odmian odpornych. W obydwu latach badań (2015-2016) stwierdzono dodatnią korelację między zawartością cukrów redukujących a liczebnością wciornastków w całym sezonie wegetacyjnym oraz ujemną korelację między zawartością fenoli ogółem a procentem uszkodzonej powierzchni liści przez wciornastki. Jedynie w 2015 stwierdzono, że wyższa zawartość cukrów rozpuszczalnych i sacharozy w liściach cebuli była istotnie ujemnie skorelowana z procentem uszkodzonej powierzchni liści cebuli. Podejrzewamy również, że cieńsza warstwa epidermy, mniejsza powierzchnia komórek epidermalnych i mezofilnych oraz mniejsza średnica wiązek naczyniowych mogą sprzyjać odporności odmian cebuli na wciornastki. Odnotowano, iż żerowanie wciornastków spowodowało obniżenie zawartości cukrów rozpuszczalnych i sacharozy w liściach wszystkich odmian cebuli, jednak istotny spadek wykazano w przypadku odmian 'Alibaba', 'Karmen' i 'Wenta' w 2015 oraz 'Kristine' i 'Niagara F₁' w 2016 roku. Z kolei, odmiany: 'Bila', 'Kristine', 'Polanowska', 'Tęcza' i 'Wenta' w 2015 roku oraz 'Tęcza' w 2016 roku, zareagowały na żerowanie wciornastków istotnym wzrostem zawartości cukrów redukujących. Jedynie istotny spadek zawartości cukrów redukujących stwierdzono u odmiany 'Bila' i 'Wenta' w 2016 roku. W 2015 roku, wszystkie odmiany odpowiedziały na żerowanie wciornastków istotnym wzrostem zawartości fenoli ogółem w liściach, natomiast w 2016 roku, istotny wzrost tych związków stwierdzono w liściach odmian: 'Bila', 'Karmen', 'Polanowska', 'Tęcza' i 'Wenta'. Żerowanie wciornastka tytoniowca wpłynęło negatywnie na zawartość barwników roślinnych w liściach cebuli zwyczajnej. W obydwu latach stwierdzony istotny spadek zawartości chlorofilu a w liściach wszystkich odmian cebuli zwyczajnej, z wyjątkiem odmian 'Alibaba', 'Niagara F₁' i 'Tęcza' w 2015 roku. Istotny spadek chlorofilu b stwierdzono w liściach odmian 'Kristine', 'Niagara F₁' i 'Wenta' w 2015 roku oraz w liściach wszystkich odmian z wyjątkiem odmiany 'Polanowska' w 2016 roku. Z kolei istotny spadek karotenoidów obserwowano w liściach odmiany 'Bila' i 'Wenta' w 2015 roku oraz w liściach wszystkich odmian w 2016 roku.

3. Summary

The research aimed to determine the species composition, abundance, sex ratio, and seasonal dynamics of thrips (Thysanoptera) occurrence on eight cultivars of common onion *Allium cepa* L. and one cultivar of Welsh onion *Allium fistulosum* L, to assess the degree of colonization, development, and damage of the onion thrips (*Thrips tabaci* Lind.) on onion cultivars and to clarify some morphological, anatomical and biochemical features influencing the colonization and feeding of thrips on this plant. This research has made it possible to select onion cultivars for cultivation that are least infested at the beginning and throughout the growing season and where the onion thrips develop the weakest and cause the least damage, and to learn about the factors of increased susceptibility of some onion cultivars to feeding, colonization, and development of onion thrips. The experiment was also aimed at investigating how the feeding of the onion thrips alters the content of selected plant biochemical components.

In the years 2014-2016, field experiments were conducted at the Experimental Station of the University of Agriculture in Krakow, located in Mydlniki near Krakow. Eight cultivars of onion ('Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁', 'Polanowska', 'Tęcza' and 'Wenta') and one cultivar of Welsh onion ('Kroll') were used in the experiments. Seeds of each cultivar were sown in four replications in 3 m × 4 m (12 m²) plots.

Entomological observations on the species composition, abundance, population dynamics of thrips, and their harmfulness to onions were performed at two weekly intervals fortnightly intervals in 2014 and weekly in 2015-2016. Thrips were collected from plots using a standard entomological sweeping net and also collected directly from onion leaves. Thrips were then prepared and determined under laboratory conditions. In this paper, the degree of damage to onion leaves caused by feeding thrips was estimated and the effect of mechanical damage caused by feeding individuals of onion thrips on the content of selected biochemical compounds (soluble sugars, reducing sugars, and sucrose as well as chlorophyll a and b and carotenoids) in onion leaves was assessed. To understand the factors affecting the colonization, abundance, and feeding of the onion thrips, the content of sugars (soluble, reducing, and sucrose), total phenols in the leaves were determined and some features of their anatomical structure were analysed. Onion leaf colour parameters were also measured using a spectrophotometer (Konica Minolta Chroma Meter CM-2600d) including CIELAB (CIE 1976 L*a*b*) and CIE L*C*h* colour spaces.

In experiments carried out in 2014-2015, it was found that on *A. cepa* cultivars the most abundant species was the onion thrips followed by the flower thrips (*Frankliniella intonsa* Trybom), while the reverse order was observed Welsh onions. The third most abundant species collected was the predatory thrips species (*Aeolothrips intermedius* Bagnall). It was also reported that in these three most abundant thrips species, the populations were mainly formed by females. The most populated cultivar by thrips turned out to be 'Kroll' of the Welsh onion, while the cultivars of common onions in the following years showed a different degree of attractiveness for thrips. Furthermore, it was observed that the occurrence of the three most abundant thrips species varied during the growing season. As a general rule, the onion thrips was most abundant in June, while the percentages of the flower thrips and the predatory thrips *Aeolothrips intermedius* increased in July.

During 2-year research in 2015-2016, the leaf colour of the tested onion cultivars was observed to influence their colonization by migrating individuals of the onion thrips in the early growing season. It was observed that higher value of lightness parameter L^* , coordinate b^* , colour saturation (C^*), hue angle (h^*), and lower value of coordinate (a^*) were significantly correlated with the number of thrips. It was concluded that the intensive vivid green-yellowish colour of the leaves of susceptible cultivars: 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁', and 'Polanowska' may have been responsible for their increased attractiveness to migrating thrips. In this paper, two cultivars were selected 'Tęcza' and 'Wenta', with darker green-grey-yellowish leaves, as resistant (not very attractive) to colonization by onion thrips in the beginning period of their colonization.

In 2015-2016, it was found that the cultivars of *A. cepa* differ in their susceptibility to colonization, development, and the degree of leaf damage caused by foraging individuals of onion thrips. The cultivar 'Wenta' was considered to be moderately resistant to onion thrips development and resistant to its feeding. In turn, the cultivar 'Tęcza' was resistant to the development of thrips, unfortunately, was susceptible to feeding by these pests. The other six cultivars: 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁', and 'Polanowska' were susceptible to both development and foraging of onion thrips, while 'Niagara F₁' was highly susceptible to development, and the cultivar 'Polanowska' for thrips feeding. All cultivars of *A. cepa* susceptible to thrips development and feeding were also susceptible to colonization by migrating adult thrips during early onion plant development, with 'Niagara F₁' being the most attractive. In contrast, the cultivar 'Tęcza' was resistant and the cultivar 'Wenta' was moderately resistant to colonization by migrating thrips.

The results of the research indicate that the resistance of some *A. cepa* cultivars to the development and feeding of thrips may be related to the mechanism of antixenosis and/or antibiosis, which in turn may be related to the content of sugars and phenols in the leaves of resistant cultivars. In both years of the study (2015-2016) a positive correlation was found between the content of reducing sugars and the abundance of thrips throughout the growing season, and a negative correlation between the content of total phenols and the percentage of damaged leaf area by thrips. Only in 2015, it was observed that the higher content of soluble sugars and sucrose in onion leaves was significantly negatively correlated with the percentage of the damaged area of onion leaves. We also suspect that a thinner epidermal layer, a smaller surface area of epidermal and mesophylic cells, and a smaller diameter of vascular bundles may contribute to the resistance of onion cultivars to thrips. It was noted that thrips feeding caused a reduction in the content of soluble sugars and sucrose in the leaves of all onion cultivars, however, a significant decrease was found for the 'Alibaba', 'Karmen' and 'Wenta' cultivars in 2015 and 'Kristine' and 'Niagara F₁' in 2016. In turn, the cultivars: 'Bila', 'Kristine', 'Polanowska', 'Tęcza' and 'Wenta' in 2015 and 'Tęcza' in 2016 reacted to thrips feeding with a significant increase in the content of reducing sugars. Only a significant decrease in reducing sugars was found in the cultivars 'Bila' and 'Wenta' in 2016. In 2015, all cultivars responded to thrips feeding with a significant increase in total phenolic content in leaves, while in 2016, a significant increase in these compounds was observed in the leaves of cultivars: 'Bila', 'Karmen', 'Polanowska', 'Tęcza' and 'Wenta'. Thrips feeding decreased the concentration of plant pigment in leaves of *A. cepa*. In both years, a significant decrease in chlorophyll content was recorded in the leaves of all cultivars of *A. cepa* except 'Alibaba', 'Niagara F₁', and 'Tęcza'. A significant decrease in chlorophyll b was found in leaves of the cultivars 'Kristine', 'Niagara F₁', and 'Wenta' in 2015 and all cultivars except 'Polanowska' in 2016. In contrast, a significant decrease in carotenoids was observed in the leaves of 'Bila' and 'Wenta' in 2015 and in all cultivars in 2016.

4. Wprowadzenie

Cebula jest rośliną uprawianą na całym świecie, głównie w strefie klimatu umiarkowanego i ciepłego (Brewster 2008). Konsumenci wysoko cenią to warzywo przede wszystkim za właściwości prozdrowotne oraz walory smakowe (Griffiths 2002, Teshika i in. 2019). Także w Polsce, cebula jest zaliczana do warzyw o dużym znaczeniu gospodarczym. Roczny zbiór cebuli wynosi 651,3 tys. ton, co czyni Polskę wiodącym producentem cebuli wśród krajów Unii Europejskiej, zaraz po Holandii i Hiszpani (World Onion Production by Country 2020).

Produkcja warzyw w uprawie polowej, w tym cebuli, narażona jest na szereg niekorzystnych czynników zewnętrznych abiotycznych i biotycznych (Kalbarczyk i in. 2011), zwanych ryzykiem produkcyjnym, które wpływają na wielkość i wartość produkcji (Smolik 2021). Takimi biotycznymi czynnikami są m. in. choroby i szkodniki. Szczególnie groźnym szkodnikiem cebuli na całym świecie jest wciornastek tytoniowiec *Thrips tabaci* Lindeman 1889 (Thysanoptera: Thripidae) (Lewis 1997, Diaz-Montano i in. 2011). W Polsce na duże znaczenie wciornastka tytoniowca w uprawie cebuli jadalnej wskazali Szwejska i Wrzodak (2009), z kolei wstępne badania nad jego występowaniem i podatnością odmian cebuli na zasiedlenie przez tego szkodnika prowadzili Pobożniak i in. (2016). Szkodnik ten jest trudny do zwalczania ze względu na mikroskopijne rozmiary ciała, szybki rozwój oraz masowe naloty na uprawy. Larwy oraz osobniki dorosłe wyrządzają szkody bezpośrednie i pośrednie (Lewis 1973, Diaz-Montano i in. 2011). W okresie wegetacji żerują na całej nadziemnej części rośliny. Najczęściej można je spotkać w pobliżu pochew liściowych lub w miejscach, gdzie liście szczypioru załamują się (Lewis 1997, Gill i in. 2015).

Szkodliwość bezpośrednia wciornastków głównie polega na nakłuwaniu tkanek liści i wyssaniu z nich ich zawartości. W miejscach nakłucia puste przestrzenie uszkodzonych komórek wypełniają się powietrzem tworząc na liściach szczypioru charakterystyczne srebrzysto-białe przebarwienia. Przy dużym nasileniu szkodnika plamy zlewają się ze sobą zajmując coraz większą powierzchnię liścia. Powoduje to zmniejszenie zawartości chlorofilu i obniżenie zdolności roślin do przeprowadzenia procesu fotosyntezy, a także zakłócenie transportu składników odżywczych do organu spichrzowego (Lewis 1997, Boateng i in. 2014, Gill i in. 2015). Uszkodzenia powodowane przez wciornastki mogą znacznie obniżyć plon cebuli od 22% (Ghosheh i in. 2000), przez 30% (Rueda i in. 2007), 35-43% (Fournier i in. 1995), do nawet 60% (Waiganjo i in. 2008).

Wciornastek tytoniowiec jest również wektorem wirusów, między innymi wirusa żółtej plamistości (IYSV), którego najczęściej przenosi do upraw cebuli (Diaz-Montano 2010, Leach i in. 2019). Jego żerowanie otwiera również drogi do infekcji bakteryjnych i grzybowych (Dutta 2014, Thind 1982). Aby temu zapobiec, koniecznym jest zwalczanie wciornastka tytoniowca. Wymaga to częstego stosowania insektycydów (Alston i Drost 2008), czego niefortunnym skutkiem jest wzrost odporności na powszechnie stosowane pyretroidy i związki fosforoorganiczne (MacIntyre Allen i in. 2005, Shelton i in. 2006), a także metomyl, oksamyl (karbaminiany), abamektynę (Adesanya i in. 2020) oraz spinetoram (Moretti i in. 2019).

Zapewnienie wysokiej jakości i standardów bezpieczeństwa produktów żywnościowych, a także rosnące wymagania konsumentów sprawiają, że producenci produktów ogrodniczych muszą stosować nowoczesne systemy uprawy i ochrony roślin, których założeniem jest m. in. wykorzystywanie odpornych odmian roślin na choroby i szkodniki (Kopiński i Czernyszewicz 2020).

Wśród mechanizmów odporności roślin żywicielskich wyróżnia się m. in. antyksenozę i antybiozę (Painter 1951, Kogan i Ortman 1978). Antyksenozą, inaczej brak akceptacji, to mechanizm odpornościowy związany z wzajemnym oddziaływaniem na siebie rośliny-gospodarza i szkodnika we wstępnym okresie zasiedlania rośliny. Rośliny żywicielskie dzięki cechom morfologicznym, anatomicznym lub biochemicznym stają się nieatrakcyjne i nieodpowiednie dla szkodnika, który je omija lub po krótkim czasie je opuszcza (Painter 1951, Kogan i Ortman 1978). Drugim występującym u roślin mechanizmem odpornościowym jest antybioza. Mechanizm antybiozy polega najczęściej na tym, że substancje zawarte w odpornej odmianie lub pewne cechy anatomiczne niekorzystnie wpływają na procesy życiowe owada m.in. na płodność, masę ciała, rozwój i powodują zwiększoną śmiertelność (Scott Brown 2002). Związane jest to z nieodpowiednim składem ilościowym i jakościowym substancji pokarmowych, a także obecnością wtórnych metabolitów, które utrudniają przyswajalność pokarmu, bądź hamują jego pobieranie (Dąbrowski 1988, Pobożniak i Koschier 2014, Leiss i in. 2013, Steenbergen i in. 2018).

Zanim szkodnik wejdzie w bezpośrednią interakcję z rośliną żywicielską, najpierw dokonuje wstępnej selekcji roślin (Smith 2005). W celu lokalizacji rośliny-gospodarza owad wykorzystuje do tego bodźce fizykochemiczne, które odbiera za pomocą receptorów wzrokowych, węchowych, smakowych i czuciowych (Diaz-Montano i in. 2012, Fail i in. 2013 oraz Koschier i in. 2002). Zarówno mechanizm antyksenozy, jak i antybiozy, mają istotne

znaczenie w konstituowaniu się ogólnej odporności roślin (Diaz-Montano 2010). Odporne odmiany charakteryzują się pewnymi cechami morfologicznymi, anatomicznymi lub biochemicznymi, które stanowią pierwszą linię obrony przed atakiem i rozwojem agrofagów (Smith 2005, Reeves 2011).

Fail i in. (2008, 2013) w przeprowadzonych badaniach nad antyksenotyczną odpornością różnych odmian kapusty potwierdzili, że mechanizm ten pełni istotną funkcję w odporności odmian kapusty na uszkodzenia powodowane przez wciornastka tytoniowca. Dowiedli oni również, że barwa liści, a także współczynnik odbicia światła to czynniki, które wpływają na dokonywanie wyboru rośliny żywicielskiej przez wciornastki w procesie zasiedlania roślin. Odporne odmiany kapusty białej charakteryzowały się żółtozieloną barwą liści (Fail i in. 2008) oraz większą intensywnością odbicia światła (Bálint i in. 2013, Fail i in. 2013). Z kolei Pobożniak i Świdorski (2011) również stwierdzili, iż intensywność zielonej barwy liści grochu jest ważnym czynnikiem, który warunkował atrakcyjność tych roślin dla wciornastków. Z kolei, w badaniach przeprowadzonych na roślinach cebuli, Diaz-Montano i in. (2010, 2012) udokumentowali istnienie mechanizmu antybiozy i/lub antyksenozy u odmian cebuli o żółto-zielonej barwie liści, o niższym współczynniku odbicia światła.

Da Silva i in. (2015) stwierdzili, że cieńsza kutykula, większa ilość włosków epikutikularnych na powierzchni liści oraz większa liczba aparatów szparkowych determinuje odporność cebuli na wciornastka tytoniowca. Również cechy morfologiczne roślin mogą wpływać na odporność np. odmiany cebuli, u których środkowe liście tworzyły szerszy kąt środkowy i miały bardziej okrągłe liście, były bardziej odporne na żerowanie wciornastka tytoniowca (Da Silva i in. 2015). Alimousavi i in. (2007), Basri i Ansari (2021), Hudák i Péntes (2004) oraz Ibrahim i Adesiyun (2009) stwierdzili, iż szeroki kąt między dwoma najbardziej wewnętrznymi liśćmi, okrągły kształt przekroju poprzecznego blaszki liściowej oraz większa w pionie odległość między nimi wpływa na redukcję populacji wciornastka tytoniowca na cebuli poprzez ograniczenie do minimum larwom środowiska ochronnego przed ich wrogami i niekorzystnymi warunkami pogodowymi.

Badania nad biochemicznymi podstawami odporności roślin, w których określano wpływ zawartości niektórych metabolitów na występowanie i żerowanie wciornastków wskazują, że stanowią one ważny element mechanizmu antybiozy i/lub antyksenozy roślin na występowanie tych szkodników. W pracach Njau i in. (2017) oraz Bhone i in. (2016) odnotowano istotną dodatnią, korelację między zawartością cukrów ogółem a liczbą występujących szkodników na liściach cebuli. Również wysokie stężenie cukrów redukujących

w liściach stwierdzono w przypadku odmian cebuli bardziej atrakcyjnych dla wciornastków (Srinivas i in. 2008 oraz Bhonde i in. 2016). Identyczne spostrzeżenia poczyniono w przypadku, takich roślin jak groch czy kapusta, gdzie w pracach Pobożniak i Koschier (2014), a także Žnidarčič i in. (2007) rozwój populacji wciornastka tytoniowca zależał od zawartości sacharozy w liściach. W determinowaniu odporności roślin na wciornastki biorą udział także inne metabolity wtórne. W literaturze związki fenolowe opisane są jako jedne z bardziej znaczących czynników w mechanizmie obronnym roślin przed fitofagami (Akhtari 2014). Bhonde i in. (2016) podają, że odporne na wciornastka tytoniowca odmiany cebuli charakteryzowały się wysoką zawartością fenoli ogółem. Podobne rezultaty badań otrzymali Njau i in. (2017) oraz Akhtari (2014).

Pomimo przeprowadzenia wielu badań nad odpornością roślin cebuli na występowanie i żerowanie wciornastków nadal nie udało się uzyskać jednoznacznej odpowiedzi dotyczącej mechanizmów jej działania. Należy przypuszczać, że oprócz wymienionych cech roślin, również inne czynniki mogą warunkować odporność cebuli na wciornastka tytoniowca. Potrzebne są jednak bardziej wnikliwe obserwacje i badania, które pozwolą zrozumieć to szerokie zagadnienie.

5. Hipotezy badawcze i cele prowadzonych badań

Przeprowadzone prace eksperymentalne, treści merytoryczne i dyskusja wyników, przedstawione w rozprawie doktorskiej, miały na celu weryfikację następujących hipotez badawczych:

1. Testowane odmiany cebuli zwyczajnej (*Allium cepa* L.) i cebuli siedmiolatki (*Allium fistulosum* L.) są zasiedlane przez różne gatunki wciornastków i różnią się między sobą stopniem zasiedlenia przez nie w okresie wegetacji cebuli.
2. Zabarwienie liści cebuli zwyczajnej ma wpływ na różnice w stopniu zasiedlenia testowanych odmian cebuli zwyczajnej przez migrujące osobniki wciornastka tytoniowca (*Thrips tabaci* Lind) w początkowym okresie wegetacji roślin.
3. Testowane odmiany cebuli zwyczajnej różnią się między sobą podatnością na zasiedlenie i uszkodzenia spowodowane żerowaniem szkodliwego gatunku wciornastka tytoniowca podczas całego okresu wegetacyjnego roślin.
4. Budowa anatomiczna oraz skład biochemiczny liści testowanych odmian cebuli zwyczajnej ma wpływ na ich podatność i/lub odporność na zasiedlenie i uszkodzenia spowodowane przez żerujące osobniki wciornastka tytoniowca.
5. Uszkodzenia mechaniczne spowodowane przez żerujące osobniki wciornastka tytoniowca wpływają na zmianę zawartości niektórych składników biochemicznych roślin.

W celu weryfikacji postawionych hipotez badawczych wyznaczono następujące cele badawcze:

Publikacja 1:

1. Określenie składu gatunkowego, liczebności i udziału procentowego wciornastków na ośmiu odmianach cebuli zwyczajnej i jednej odmianie cebuli siedmiolatki.
2. Ustalenie sezonowej fluktuacji najliczniej występujących gatunków wciornastków.
3. Ustalenie stosunku płci u najliczniej występujących gatunków wciornastków.

Publikacja 2:

1. Określenie korelacji pomiędzy zbadanymi parametrami barwy liści ośmiu testowanych odmian cebuli zwyczajnej a liczbą dorosłych, migrujących osobników wciornastka tytoniowca zasiedlających rośliny na początku okresu wegetacji.
2. Wytypowanie odmian cebuli zwyczajnej o wysokim stopniu antyksenotycznej odporności podczas zasiedlania ich przez migrujące osobniki wciornastka tytoniowca.

Publikacja 3:

1. Ocena stopnia odporności ośmiu testowanych odmian cebuli jadalnej na: (1) zasiedlenie przez migrujące wciornastki w początkowym okresie wegetacji roślin (*engl. resistance to thrips colonization by migrating adults thrips*), (2) rozwój wciornastków w całym okresie wegetacji roślin (*engl. resistance to thrips abundance throughout the growing season*) oraz (3) odporności na żerowanie wciornastka tytoniowca w całym okresie wegetacji roślin (*engl. resistance to thrips damage throughout the growing season*).
2. Określenie korelacji pomiędzy zawartością wybranych związków biochemicznych w liściach testowanych odmian cebuli a liczbą zasiedlających je wciornastków oraz stopniem uszkodzenia roślin przez żerujące wciornastki.
3. Określenia korelacji pomiędzy niektórymi cechami budowy anatomicznej liści cebuli a liczbą zasiedlających je wciornastków i stopniem uszkodzenia roślin przez żerujące wciornastki.
4. Ocena wpływu uszkodzeń mechanicznych spowodowanych przez żerujące osobniki wciornastka tytoniowca na zawartość wybranych związków biochemicznych w liściach testowanych odmian cebuli.

6. Materiały i metody

6.1. Materiał roślinny

W badaniach wykorzystano osiem odmian cebuli zwyczajnej (*A. cepa*) oraz jedną odmianę cebuli siedmiolatki (*A. fistulosum*). Wszystkie nasiona cebuli zwyczajnej pochodziły z polskich hodowli: PlantiCo Hodowla i Nasiennictwo Ogrodnicze Zielonki sp. z o.o. ('Alibaba', 'Bila', 'Kristine', 'Niagara F₁' i 'Wenta'), Krakowska Hodowla i Nasiennictwo Ogrodnicze POLAN Spółka z o.o. ('Karmen' i 'Polanowska') oraz Spójnia Hodowla i Nasiennictwo Ogrodnicze sp. z o.o. ('Tęcza'). Odmiana 'Kroll' cebuli siedmiolatki pochodziła z hodowli PlantiCo Hodowla i Nasiennictwo Ogrodnicze Zielonki sp. z o.o. Charakterystyka odmian została podana w tabeli 1.

Tabela 1. Charakterystyka badanych odmian cebuli zwyczajnej (*Allium cepa* L.) oraz cebuli siedmiolatki (*Allium fistulosum* L.).

Gatunek/ Odmiana	Wczesność/ plenność	Wielkość cebul	Kształt cebul	Barwa suchej łuski	Przyleganie łuski	Przydatność
PlantiCo Hodowla i Nasiennictwo Ogrodnicze Zielonki sp. z o.o.						
<i>Allium cepa</i> 'Alibaba'	średniopóźna, plenna	duże	kuliste	biała	dobrze przylegająca łuska	bezpośrednie spożycie, produkcja suszu
<i>Allium cepa</i> 'Kristine'	średniopóźna, plenna	duże	kuliste	złota	dobrze przylegająca łuska	bezpośrednie spożycie, produkcja suszu, długotrwałe przechowywanie
<i>Allium cepa</i> 'Niagara F ₁ '	średniopóźna, bardzo plenna	duże	kuliste	ciemnozłota	dobrze przylegająca łuska	bezpośrednie spożycie, długotrwałe przechowywanie
<i>Allium cepa</i> 'Wenta'	średniopóźna, plenna	duże	lekko spłaszczo- kuliste	ciemnoczerwona	dobrze przylegająca łuska	bezpośrednie spożycie
<i>Allium cepa</i> 'Bila'	późna, bardzo plenna	duże	kulisto- wydłużone	ciemnożółta- jasnobrązowej	dobrze przylegająca łuska	bezpośrednie spożycie, produkcja suszu, długotrwałe przechowywanie
<i>Allium fistulosum</i> 'Kroll'	wczesna	-	podługowate, ściśle przylegające do siebie zgrubienia	biała	-	bezpośrednie spożycie w postaci mięsistych, rurkowatych liści

Tabela 1 cd. Charakterystyka badanych odmian cebuli zwyczajnej (*Allium cepa* L.) oraz cebuli siedmiolatki (*Allium fistulosum* L.).

Gatunek/ Odmiana	Wczesność/ plenność	Wielkość cebul	Kształt cebul	Barwa suchej łuski	Przyleganie łuski	Przydatność
Krakowska Hodowla i Nasiennictwo Ogrodnicze POLAN sp. z o.o.						
<i>Allium cepa</i> 'Karmen'	średniowczesna, plenna	duże	kuliste	czerwona	dobrze przylegająca łuska	bezpośrednie spożycie, długotrwałe przechowywanie
<i>Allium cepa</i> 'Polanowska'	późna, plenna, z silnym nalotem woskowym	średnie- dużych	kulisto- szerokojajowate	żółtobrazowa	dobrze przylegająca łuska	przetwórstwo, długotrwałe przechowywanie
Spójnia Hodowla i Nasiennictwo Ogrodnicze sp. z o.o.						
<i>Allium cepa</i> 'Tęcza'	bardzo wczesna	średnie- dużych	kulisto- spłaszczone	ciemnożółta	dobrze przylegająca łuska	bezpośrednie spożycie, krótkotrwałe przechowywanie

6.2. Teren badań polowych

W latach 2014-2016 prowadzono doświadczenia polowe w Stacji Doświadczalnej Uniwersytetu Rolniczego w Krakowie, położonej w Mydlnikach (okolice Krakowa, południowa Polska, 50°04'N, 19°51'E, 207 m n.p.m.) na typowej glebie brunatnej o pH 6,5 i zawartości węgla organicznego 18 g · kg⁻¹. Eksperyment założono w układzie losowanych bloków z czterema powtórzeniami. Powierzchnia poletek doświadczalnych wynosiła 12 m² (3 × 4 m²) a odległość między poletkami wynosiła 1 m. Nasiona wysiano (25 kg · ha⁻¹) w rzędy w odległości 0,3 m od siebie w dniach 6 kwietnia 2014, 10 kwietnia 2015 oraz 6 kwietnia 2016 roku. Poletka doświadczalne nawożono zgodnie z zaleceniami Integrowanej Produkcji dla cebuli w uprawie polowej. Przez cały sezon poletka były utrzymywane w stanie wolnym od chwastów. W trakcie trwania doświadczenia na poletkach nie wykonywano żadnych zabiegów chemicznych, a odchwaszczanie wykonywano ręcznie. W otoczeniu poletka doświadczalnego znajdowały się następujące rośliny: ziemniaki, zioła, buraki ćwikłowe, kapusta biała, cukinia i dynia. Ponadto w najbliższym otoczeniu rosły słoneczniki i rośliny ozdobne, takie jak nagietek i dalia. W odległości około 0,5-1 km od obiektu doświadczalnego uprawiano zboża i rzepak.

6.3. Zastosowane metody badawcze

Metody badawcze, które zastosowano w poszczególnych etapach doświadczeń zostały szczegółowo opisane i zamieszczone w rozdziale 'Materials and Methods' w każdej z publikacji będącej przedmiotem rozprawy doktorskiej.

Poniżej przedstawiono wykaz metod wykorzystanych w pracy doktorskiej:

- Analizy entomologiczne prowadzono przez cały okres wegetacji cebuli w odstępach około 2 tygodniowych w 2014 roku i cotygodniowym w latach 2015-2016. Wciornastki odławiano z liści cebuli za pomocą standardowego czerpaka entomologicznego o średnicy 35 cm wykonując 25 zamachów z każdego poletka (publikacja 1-2) oraz bezpośrednio z 10-ciu losowo zebranych roślin z każdego poletka (publikacja 1-3). Wciornastki odłowione z każdego poletka za pomocą czerpaka entomologicznego były umieszczane w odpowiednio wcześniej opisanym worku foliowym z zaznaczeniem numeru poletka oraz daty odłowu. W przypadku roślin, 10 losowo wybranych roślin, umieszczano w jednym worku foliowym, który wcześniej był opisany. Następnie worki były transportowane do laboratorium, gdzie za pomocą pędzelka (nr 1) wciornastki były zbierane i umieszczane w fiolkach z płynem konserwującym. W celu uniknięcia pominięcia larw wciornastków liście były przeglądane pod mikroskopem stereoskopowym (publikacje 1,3).
- Identyfikację gatunkową wciornastków przeprowadzono w warunkach laboratoryjnych. W tym celu wykonywano preparaty mikroskopowe wciornastków zgodnie z techniką opisaną przez Zawirską (1994), a następnie oznaczano okazy do gatunku z wykorzystaniem kluczy: Zawirska (1994), zur Strassen (2003) (osobniki dorosłe) (publikacja 1-3) i Kucharczyk (2010) (larwy) (publikacja 1, 3).
- Instrumentalne i numeryczne określenie barwy liści cebuli wykonano za pomocą przenośnego spektrofotometru (Konica Minolta Chroma Meter CM-2600d) z uwzględnieniem przestrzeni barw CIELAB (CIE 1976 L*a*b*) i CIE L*C*h* (publikacja 2).
- Oszacowano stopień uszkodzenia liści cebuli spowodowanych przez żerujące wciornastki (publikacja 3).
- Wykonano biochemiczne analizy liści nieuszkodzonych i uszkodzonych cebuli przez żerujące osobniki wciornastka tytoniowca:
 - oznaczono zawartość cukrów rozpuszczalnych metodą antronową,
 - oznaczono zawartość cukrów redukujących metodą heksacyjanożelazianową,
 - obliczono zawartość sacharozy jako różnicę między zawartością cukrów rozpuszczalnych ogółem a zawartością cukrów redukujących,
 - oznaczono zawartość związków fenolowych ogółem metodą Folin-Ciocalteu,

- oznaczono zawartość chlorofilu a i b oraz karotenoidów ogółem z wykorzystaniem spektrofotometru JASCO V-530 UV/Vis do pomiaru widm wykonanych ekstraktów (publikacja 3).
- Wykonano badania anatomicznej budowy liści cebuli (publikacja 3).
- Dobrano metody statystycznej analizy wyników (publikacja 1-3).

7. Omówienie przeprowadzonych badań i ich wyników

7.1. Publikacja nr 1

Olczyk, M., Pobożniak, M. (2020). Thrips (Thysanoptera) associated with onion (*Allium cepa* L.) and Welsh onion (*Allium fistulosum* L.). *Folia Horticulturae* 32(2), 319-335. <https://doi.org/10.2478/fhort-2020-0028>.

W publikacji określono skład gatunkowy oraz liczebność wciornastków (Thysanoptera) na ośmiu odmianach cebuli zwyczajnej (*A. cepa*) oraz jednej odmianie cebuli siedmiolatki (*A. fistulosum*). W pracy określono również stosunek płci u trzech najliczniej występujących gatunków wciornastków oraz sezonową fluktuację ich występowania.

Trzyletnie obserwacje wykazały, że liczba odłowionych wciornastków i ich udział w zebranych materiale z badanych odmian cebuli zwyczajnej i siedmiolatki różniła się w zależności od gatunku cebuli, odmiany oraz roku badań.

W trakcie trzyletnich badań (2014-2016) z ośmiu odmian cebuli zwyczajnej i jednej odmiany cebuli siedmiolatki odłowiono 10 gatunków wciornastków a ich liczba wahała się od sześciu w 2014 roku do dziewięciu w 2015 i 2016 roku. Większej liczbie odłowionych osobników towarzyszyła z reguły zwiększona liczba gatunków (Tabela 2).

Tabela 2. Skład gatunkowy wciornastków (Thysanoptera) zebranych z cebuli zwyczajnej i cebuli siedmiolatki w latach 2014-2016, Mydlniki.

Gatunek	Rok			Suma
	2014	2015	2016	
Wciornastek tytoniowiec <i>Thrips tabaci</i> Lindeman, 1889	1829	12038	5793	19660
Wciornastek kwiatowiec <i>Frankliniella intonsa</i> Trybom, 1895	1740	6947	2775	11462
Wciornastek płowy <i>Thrips flavus</i> Schrank, 1776	50	14	2	66
Wciornastek różówek <i>Thrips fuscipennis</i> Haliday, 1836	-	18	134	152
Wciornastek lisiogonek <i>Chirothrips hamatus</i> Trybom, 1895	-	26	98	124
<i>Chirothrips manicatus</i> Haliday, 1836	-	-	43	43
Wciornastek pstrokacz <i>Aeolothrips intermedius</i> Bagnall, 1934	128	368	823	1319

Tabela 2 cd. Skład gatunkowy wciornastków (Thysanoptera) zebranych z cebuli zwyczajnej i cebuli siedmiolatki w latach 2014-2016, Mydlniki.

Gatunek	Rok			Suma
	2014	2015	2016	
Wciornastek złocienowiec <i>Haplothrips leucantemi</i> Schrank, 1781	30	1	16	47
Wciornastek zbożowy kwietniczek <i>Haplothrips aculeatus</i> Fabricius, 1803	14	8	141	163
Wciornastek koniczynowiec <i>Haplothrips niger</i> Osborn, 1883	-	30	-	30

We wszystkich latach najliczniejszym gatunkiem był wciornastek tytoniowiec (*Thrips tabaci*), a następnie wciornastek kwiatowiec (*Frankliniella intonsa*). Trzecim pod względem liczby odłowionych osobników był wciornastek pstrokacz (*Aeolothrips intermedius*). Pozostałe gatunki były odławiane w znacznie mniejszej liczbie, a jedynie w 2016 roku obserwowano liczniejsze występowanie wciornastka różówka (*Thrips fuscipennis*) oraz wciornastka zbożowego kwietniczka (*Haplothrips aculeatus*) i wciornastka lisiogonka (*Chirothrips hamatus*), co prawdopodobnie związane było z obecnością kwitnących roślin i zbóż w sąsiedztwie poletek doświadczalnych (Tabela 2).

W 2014 roku z wszystkich testowanych odmian cebuli zwyczajnej i jednej odmiany cebuli siedmiolatki odłowiono 3 tyś. 791 osobników wciornastków (larw i dorosłych). Największą liczbę wciornastków, aż 932 osobników zebrano z cebuli siedmiolatki odmiany 'Kroll', podczas gdy z cebuli zwyczajnej liczba odłowionych wciornastków wahała się od 310 osobników na odmianie 'Niagara F₁' do 430 na odmianie 'Polanowska'. Na większości odmian cebuli zwyczajnej najliczniej występował wciornastek tytoniowiec z udziałem od 51,0% na 'Wenta' do 78,85% na 'Karmen'. Jedynie na odmianie 'Kristine' jego udział procentowy wynosił 45,6% i był nieco mniejszy niż wciornastka kwiatowca, którego udział w zebranych materiale na tej odmianie wynosił 48,5%. Z kolei na odmianie 'Kroll' cebuli siedmiolatki, udział wciornastka tytoniowca w zebranych materiale stanowił zaledwie 10,6%, podczas gdy udział wciornastka kwiatowca wynosił aż 86,5%. Udział drapieżnego wciornastka pstrokacza na odmianach cebuli zwyczajnej wahał się od 1,2% na odmianie 'Tęcza' do 7,7% na odmianie 'Niagara F₁', natomiast na cebuli siedmiolatce 'Kroll' wynosił 2,2%. Udział pozostałych trzech gatunków na cebuli zwyczajnej stanowił 1,05% ogólnej liczby wciornastków zebranych, podczas gdy na cebuli siedmiolatce wynosił zaledwie 0,25%.

W 2015 roku ze wszystkich testowanych odmian cebuli zwyczajnej i siedmiolatki odłowiono 19 tys. 450 osobników. Podobnie jak w poprzednim roku, największą liczbę wciornastków (4 tys. 536 osobników) zebrano z odmiany 'Kroll' cebuli siedmiolatki. W przypadku odmian cebuli zwyczajnej liczba wciornastków wahała się od 1 tys. 475 osobników na odmianie 'Polanowska' do 2 tys. 054 na odmianie 'Niagara F₁'. Wszystkie odmiany cebuli zwyczajnej były najliczniej zasiedlone przez wciornastka tytoniowca, a jego udział w zgromadzonym materiale wahał się od 65% na odmianie 'Tęcza' do 73,8% na odmianie 'Wenta'. Drugim gatunkiem pod względem liczby zebranych osobników był wciornastek kwiatowiec z udziałem od 24,3% na odmianie 'Wenta' do 33,3% na odmianie 'Tęcza'. Z kolei na cebuli siedmiolatce 'Kroll' udział wciornastka kwiatowca był wyższy niż wciornastka tytoniowca i wynosił odpowiednio 59,2% i 39,3%. W 2015 roku drapieżny gatunek wciornastka pstrokacza na odmianach cebuli zwyczajnej stanowił od 1,7% na odmianie 'Tęcza' do 2,9% na odmianie 'Kristine', natomiast na cebuli siedmiolatce odmiany 'Kroll' wynosił zaledwie 0,9%. Udział pozostałych gatunków na odmianach cebuli zwyczajnej wynosił 0,07%, a na cebuli siedmiolatce 0,08%.

W 2016 roku zebrano łącznie 9 tys. 825 okazów wciornastków. Podobnie jak w dwóch poprzednich latach badań największą liczbę wciornastków tj. 2 tys. 458 osobników odłowiono z odmiany 'Kroll' cebuli siedmiolatki, natomiast z odmian cebuli zwyczajnej odłowiono od 232 wciornastków na odmianie 'Tęcza' do 844 osobników na odmianie 'Polanowska'. Najliczniej występującym gatunkiem na wszystkich badanych odmianach cebuli zwyczajnej był wciornastek tytoniowiec z udziałem od 58,2% na odmianie 'Wenta' do 80,3% na odmianie 'Tęcza'. W przeciwieństwie do poprzednich lat, na odmianie 'Kroll', niewielką przewagę w liczbie odłowionych osobników miał wciornastek tytoniowiec, a jego udział w całości materiału zebranego z cebuli siedmiolatki wynosił 44,1%, podczas gdy udział wciornastka kwiatowca był nieco niższy i wynosił 42,4%. Udział wciornastka kwiatowca na odmianach cebuli zwyczajnej wahał się od 10,0% na odmianie 'Tęcza' do 28,1% na odmianie 'Wenta'. Udział trzeciego gatunku pod względem liczby zebranych osobników tj. wciornastka pstrokacza wynosił od 6,9% na odmianie 'Polanowska' do 11,2% na odmianie 'Alibaba' natomiast na odmianie 'Kroll' wynosił 5,6%. Podobnie jak w ubiegłych latach, pozostałe gatunki wciornastków stanowiły tylko 3,25% na cebuli zwyczajnej i 7,9% na cebuli siedmiolatce.

W latach 2015-2016 określono stosunek płci trzech najliczniej występujących gatunków, tj. wciornastka tytoniowca, wciornastka kwiatowca i wciornastka pstrokacza.

Populację wszystkich wymienionych gatunków stanowiły głównie samice. Na odmianach cebuli zwyczajnej samice wciornastka tytoniowca stanowiły od 99,8% do 100% na przestrzeni obu lat badań. Populacja wciornastka kwiatowca również reprezentowana była głównie przez samice, które stanowiły 98,9% do 100% populacji tego gatunku. W populacji drapieżnego wciornastka pstrokacza udział samic w populacji wahał się od 87,4% do 100% w 2015 roku, natomiast w kolejnym roku był mniejszy i na większości odmian cebuli zwyczajnej wynosił od 73,5% do 78,9%, a jedynie na odmianie Tęcza wynosił 100%. Na cebuli siedmiolatce odmiany 'Kroll' udział samic w populacji wciornastka tytoniowca wynosił 99,3% w 2015 i 100% w 2016 roku, a wciornastka kwiatowca odpowiednio 97,0% i 98,0%. W populacji wciornastka pstrokacza udział samic był niższy i wynosił 87,5% w 2015 i 84,7% w 2016.

W latach 2014-2016 prześlędzono również, w jaki sposób udział trzech najliczniejszych gatunków wciornastków tj. wciornastka tytoniowca, wciornastka kwiatowca oraz wciornastka pstrokacza zmieniał się w poszczególnych miesiącach sezonu wegetacyjnego na odmianach cebuli zwyczajnej i odmianie cebuli siedmiolatki.

W 2014 roku w drugiej połowie czerwca na odmianie 'Tęcza' i 'Kroll' występował tylko wciornastek tytoniowiec, podczas gdy na pozostałych odmianach oprócz niego obecny był wciornastek kwiatowiec. Udział wciornastka tytoniowca był z reguły wyższy niż wciornastka kwiatowca i wahał się w zależności od odmiany od 58,3% na odmianie 'Wenta' do 89,9% na odmianie 'Polanowska' i jedynie na odmianie 'Alibaba' był niższy i wynosił 45,5%. W pierwszej połowie lipca najliczniejszym gatunkiem zasiedlającym wszystkie odmiany cebuli zwyczajnej był wciornastek tytoniowiec, a jego udział wynosił od 56,0% na 'Wencie' do 92,8% na 'Tęczy'. W tym czasie na cebuli siedmiolatce 'Kroll' najwyższy udział miał wciornastek kwiatowiec (69,4%). Od połowy lipca do końca sierpnia udział wciornastka tytoniowca na odmianach cebuli zwyczajnej wahał się od 25,0% ('Bila' w drugiej połowie lipca) do 87,5% ('Bila' w drugiej połowie sierpnia), natomiast jego udział na cebuli siedmiolatce był niski i nie przekraczał 11,5% (druga połowa sierpnia). Drapieżny gatunek wciornastka pstrokacza był odławiany w lipcu i sierpniu. Jego udział na cebuli zwyczajnej w lipcu wahał się 0,9% ('Karmen' w 1-szej połowie lipca) do 8,4% ('Niagara F₁' w 1-szej połowie lipca). Z kolei, w pierwszej połowie sierpnia gatunek ten nie był stwierdzany tylko na odmianie 'Tęcza' natomiast na pozostałych występował z udziałem od 5,6% na 'Wencie' do 15,8% na 'Alibabie'. W drugiej połowie sierpnia był obecny tylko na dwóch odmianach 'Kristine' i 'Niagara F₁', a jego udział w zebranych materiale wynosił odpowiednio 6,0%

i 50,0%. Na cebuli siedmiolatce w lipcu i sierpniu udział wciornastka pstrokacza nie przekraczał odpowiednio 2,0% i 3,5%.

W drugiej połowie czerwca 2015 roku większość odmian cebuli zwyczajnej było zasiedlonych wyłącznie przez wciornastka tytoniowca. Jedynie dwie odmiany cebuli zwyczajnej 'Polanowska' i 'Tęcza' oraz odmiana 'Kroll' cebuli siedmiolatki były zasiedlone odpowiednio w 71,4%, 50,0% i 80,0% przez wciornastka tytoniowca, podczas gdy resztę stanowił wciornastek kwiatowiec. W lipcu (szczególnie w drugiej połowie) udział wciornastka kwiatowca na odmianach cebuli zwyczajnej wzrósł i wahał się od 18,4% na 'Kristine' do 44,0% na 'Polanowskiej', natomiast na cebuli siedmiolatce jego udział wynosił aż 63,5%. W sierpniu na wszystkich odmianach cebuli zwyczajnej stosunek liczebności obu gatunków uległ odwróceniu i wciornastek tytoniowiec ponownie stał się najliczniejszym taksonem. Na cebuli siedmiolatce udział wciornastka tytoniowca wynosił 36,2% i 59,4% odpowiednio w pierwszej i drugiej połowie miesiąca. Podobnie jak w roku poprzednim wciornastek pstrokacz był odławiany z cebuli zwyczajnej i siedmiolatki w lipcu i sierpniu. W lipcu jego udział na cebuli zwyczajnej nie przekraczał 4,2%, a na cebuli siedmiolatce 0,9%, natomiast w sierpniu odpowiednio 7,0% i 1,9%.

W czerwcu 2016 roku udział wciornastka tytoniowca na odmianach cebuli zwyczajnej wahał się od 61,3% na 'Alibabie' do 94,1% na 'Tęczy', natomiast na odmianie cebuli siedmiolatki 'Kroll' wynosił 68,1%. Na cebuli zwyczajnej wciornastek tytoniowiec również najliczniejszy był w lipcu i jego udział w pierwszej połowie tego miesiąca wahał się od 70,5% na 'Bili' do 81,3% na 'Karmen', natomiast w drugiej połowie lipca jego udział zmalał i wynosił od 53,8% na 'Alibabie' do 72,7% na 'Kristine'. Spadek ten związany był z liczniejszym występowaniem wciornastka kwiatowca oraz wciornastka pstrokacza. Z kolei na cebuli siedmiolatce udział wciornastka tytoniowca wynosił 47,9% i 65,9% odpowiednio w pierwszej i drugiej połowie lipca. W 2016 roku wciornastek pstrokacz odławiany był z cebuli zwyczajnej i siedmiolatki już w drugiej połowie czerwca, a jego udział na cebuli zwyczajnej nie przekraczał 2,3% na 'Kristine', podczas gdy na cebuli siedmiolatce wynosił 1,5%. W lipcu i sierpniu obserwowano wzrost jego liczebności na cebuli zwyczajnej i w lipcu najwyższy był na odmianie 'Karmen' (18,6%), a w sierpniu na odmianie 'Tęcza' (43,8%). Również tendencję wzrostową wciornastka pstrokacza obserwowano na cebuli siedmiolatce, a jego udział wynosił 5,9% w lipcu i 14,9% w sierpniu.

7.2. Publikacja nr 2

Pobożniak, M., Olczyk, M., Wójtowicz, T. (2021). Relationship between colonization by onion thrips (*Thrips tabaci* Lind.) and leaf colour measures across eight onion cultivars (*Allium cepa* L.). *Agronomy* 11(5), 963. <https://doi.org/10.3390/agronomy11050963>.

W niniejszej publikacji zostały przedstawione wyniki badań polowych nad wpływem barwy liści ośmiu odmian cebuli zwyczajnej na zasiedlenie ich przez migrujące dorosłe osobniki wciornastka tytoniowca. Odmiany cebuli zostały wybrane w oparciu o wcześniej przeprowadzone badania, które wskazywały, że odmiany te różnią się między sobą stopniem zasiedlenia przez wciornastki (Pobożniak i in. 2016). W badaniach ujęto tylko migrujące osobniki dorosłe wciornastków w okresie kolonizacji roślin na początku ich wegetacji. Sposób wyznaczenia terminów ich występowania opisano w metodyce.

W latach 2015-2016 stwierdzono statystycznie istotne różnice pomiędzy średnią liczbą oraz proporcjonalną liczbą (wyrażoną w procentach) migrujących wciornastków zebranych bezpośrednio z liści testowanych odmian cebuli oraz odłowionych za pomocą czerpaka entomologicznego.

W 2015 roku istotnie wyższą średnią liczbę wciornastka tytoniowca zebrano bezpośrednio z liści odmian ‘Niagara F₁’ oraz ‘Bila’ w porównaniu z pozostałymi odmianami z wyjątkiem ‘Karmen’, ‘Kristine’ i ‘Polanowska’. W drugiej grupie jednorodnej pod względem liczby zebranych osobników znalazły się ‘Alibaba’ oraz ‘Tęcza’, natomiast ‘Wenta’ była zasiedlona przez najmniejszą liczbę wciornastków. Również istotne różnice stwierdzono w proporcjonalnej liczbie wciornastków pomiędzy odmianami najliczniej zasiedlonymi ‘Niagara F₁’ i ‘Bila’ a pozostałymi odmianami z wyjątkiem trzech ‘Karmen’, ‘Kristine’ i ‘Polanowska’. Podobne zależności stwierdzono podczas porównywania proporcjonalnej liczby wciornastków, z tą różnicą, że ‘Wenta’ nie różniła się istotnie od ‘Alibaby’ i ‘Tęczy’.

Niemal identyczną podatność odmian cebuli zwyczajnej na zasiedlenie przez migrujące wciornastki wykazano na podstawie średniej i proporcjonalnej liczby osobników odłowionych za pomocą czerpaka entomologicznego. Stwierdzono istotną różnicę pomiędzy najbardziej atrakcyjną na zasiedlenie odmianą ‘Niagara F₁’ a wszystkimi pozostałymi badanymi odmianami. Z kolei na ‘Alibaby’ i ‘Wencie’ stwierdzono najmniejszą średnią liczbę wciornastków. W przypadku proporcjonalnej liczby wciornastków do grupy istotnie najslabiej zasiedlanych odmian dołączyła ‘Karmen’.

W 2016 roku istotnie najwyższą średnią i proporcjonalną liczbę migrujących wciornastków zebrano bezpośrednio z liści sześciu odmian cebuli: 'Alibaba', 'Karmen', 'Kristine', 'Niagara F₁', 'Polanowska' oraz 'Wenta'. W drugiej grupie jednorodnej znalazła się 'Bila', natomiast najsłabiej zasiedlana była 'Tęcza'. Na podstawie liczby osobników odłowionych z cebuli za pomocą czerpaka entomologicznego wykazano, że średnia liczba wciornastków najwyższa była na odmianach 'Alibaba' i 'Niagara F₁' w porównaniu do wszystkich innych odmian z wyjątkiem 'Polanowskiej'. Odmiana 'Tęcza' była zasiedlana przez najmniejszą liczbę wciornastków, a przed nią znalazły się 'Wenta', 'Bila' i 'Kristine'. Na podstawie proporcjonalnej liczby wciornastków stwierdzono, że najbardziej atrakcyjne dla wciornastka tytoniowca podczas zasiedlenia cebuli były odmiany 'Niagara F₁', 'Alibaba' i 'Polanowska', natomiast najmniej 'Tęcza'.

W obydwu latach tj. w 2015 i 2016 stwierdzono, że odmiany cebuli różniły się istotnie między sobą wartościami wszystkich parametrów barwy liści.

W 2015 roku wartość współrzędnej L*, określającej jasność liści cebuli była najwyższa u podatnej na kolonizację przez wciornastka tytoniowca odmiany 'Bila'. Z kolei najniższą wartość tego parametru barwy stwierdzono u najmniej atrakcyjnej odmiany 'Wenta'. U wszystkich testowanych odmian cebuli wartości współrzędnej a* były ujemne, co wskazywało na dominację koloru zielonego nad czerwonym. Odmiana 'Bila' miała istotnie najniższą wartość parametru a* w porównaniu z pozostałymi odmianami. Z kolei wszystkie wartości parametru b* były dodatnie, co z kolei wskazywało na dominację barwy żółtej nad niebieską. Dla wartości współrzędnej b*, jak również dla parametru nasycenia barwy C* test Duncana pozwolił na wyodrębnienie trzech grup jednorodnych. Odmiana 'Bila' posiadała najwyższe średnie wartości współrzędnej b* i wartości wskaźnika nasycenia barwy C*. Umiarkowanie podatna odmiana 'Tęcza' znalazła się w drugiej grupie jednorodnej ze średnią wartością b*, natomiast sześć pozostałych odmian tworzyło trzecią grupę jednorodną, w której najniższą wartość współrzędnej b* stwierdzono dla odmiany 'Wenta'. Z kolei dla wartości kąta barwy h*, który jest miarą odcienia barwy istotnie najwyższą (bezwzględną) wartość uzyskały odmiany 'Bila' i 'Tęcza' o szaro-żółtawym odcieniu liści, natomiast najniższą 'Alibaba' i 'Polanowska' o odcieniu bardziej zbliżonym do żółtego koloru.

W 2016 roku dwie atrakcyjne dla wciornastków odmiany 'Alibaba' i 'Kristine' charakteryzowały się najwyższą wartością współczynnika jasności L* oraz współrzędnych barwy a* i b*. Ponadto odmiany te charakteryzowały się również najwyższym

współczynnikiem nasycenia barwy C^* , a odmiana 'Alibaba' najwyższą wartością kąta barwy h^* .

W 2015 roku stwierdzono istotnie dodatnie korelacje pomiędzy średnią i proporcjonalną liczbą wciornastków zebranych bezpośrednio z liści cebuli oraz odłowionych za pomocą czerpaka entomologicznego a wartościami parametrów jasności (L^*), nasyceniem barwy (C^*), kąta barwy (h^*) oraz wartością współrzędnej b^* . Z kolei ujemne korelacje stwierdzono pomiędzy obydwoma wskaźnikami zasiedlenia cebuli przez wciornastki a wartością współrzędnej a^* , przy czym korelacja ta nie była istotna tylko w przypadku proporcjonalnej liczby wciornastków odłowionych za pomocą czerpaka.

W 2016 roku istotnie dodatnie korelacje stwierdzono tylko pomiędzy średnią i proporcjonalną liczbą wciornastków zebranych bezpośrednio z liści cebuli a wartością L^* , b^* , C^* oraz h^* . Stwierdzono istotnie ujemną korelację pomiędzy proporcjonalną liczbą wciornastków zebranych bezpośrednio z liści a wartością współrzędnej a^* .

Reasumując, odmiany o najwyższej wartości współczynnika jasności L^* tj. 'Bila' i 'Niagara F₁' w 2015 oraz 'Alibaba' i 'Niagara F₁' w 2016 były bardzo atrakcyjne dla wciornastka tytoniowca. Przeciwnie, odmiany odporne na kolonizację przez wciornastki, takie jak 'Wenta' w 2015 i 'Tęcza' w 2016 roku miały niską wartość L^* i były ciemniejsze. Im bardziej ujemna wartość współrzędnej a^* , tym większe jest zazielenienie liści. U odmian podatnych na zasiedlenie przez wciornastki tj. 'Bila' w 2015 oraz 'Alibaba' i 'Kristine' w 2016 roku wartość a^* była istotnie niższa w porównaniu do innych odmian, a więc zielona barwa ich liści była bardziej intensywna. Równocześnie rosnąca dodatnia wartość współrzędnej b^* (zażółcenia) u podatnych odmian wskazywała, że barwa ich liści była też żółtawa. Z kolei, rosnąca wartość współrzędnej a^* u odmian odpornych jak 'Wenta' w 2015 roku i 'Tęcza' w 2016 roku, i niższa wartość współrzędnej b^* wskazywały na mniej intensywną zieloną barwę ich liści i mniej żółtawy ton. Niższa wartość współczynnika nasycenia barwy C^* u odmian odpornych oznacza, że barwa ich liści jest mniej nasycona w porównaniu z podatnymi na zasiedlenie odmianami. Różnica barwy (ΔH^*ab) i kąt barwy h^* wskazują, że barwa liści odmian najbardziej skolonizowanych przez wciornastki miała bardziej żółtawy odcień, podczas gdy u najmniej skolonizowanych odmian ich kolor był bardziej szary.

7.3. Publikacja nr 3

Pobożniak, M., Olczyk, M., Wójtowicz, T., Kamińska, I., Hanus-Fajerska, E., Kosteckga-Gugała, A., Kruczek, M. (2022). Anatomical and biochemical traits associated with field resistance of onion cultivars to onion thrips and the effect of mechanical injury on the level of biochemical compounds in onion leaves. *Agronomy* 12(1), 147. <https://doi.org/10.3390/agronomy12010147>.

W trakcie dwuletnich badań polowych (2015-2016) oceniono stopień odporności ośmiu odmian cebuli zwyczajnej na zasiedlenie ich przez migrujące dorosłe osobniki wciornastka tytoniowca na początku wegetacji roślin oraz na rozwój wciornastków i ich żerowanie w całym okresie wegetacji. Analiza statystyczna wykazała, że odmiana cebuli ma wpływ na wszystkie porównywane wskaźniki odporności roślin, tj. (1) średnią liczbę dorosłych wciornastków zasiedlających odmiany na początku okresu wegetacji, (2) średnią liczbę larw i dorosłych wciornastków występujących na roślinach w całym okresie wegetacji oraz (3) średni procent uszkodzonej powierzchni liścia przez żerujące wciornastki.

W 2015 roku wykazano, że we wczesnym okresie wegetacji roślin istotnie najliczniej zasiedlanymi przez migrujące wciornastki były odmiany ‘Alibaba’ i ‘Niagara F₁’ w porównaniu do innych odmian, z wyjątkiem trzech ‘Karmen’, ‘Kristine’ i ‘Polanowska’. Z kolei istotnie najmniejszą liczbę migrantów zebrano z odmiany ‘Wenta’. Najwyższą średnią liczbę dorosłych i larw wciornastków w całym sezonie wegetacyjnym zebrano z ‘Alibaby’ i ‘Niagary F₁’, natomiast istotnie najmniejszą z ‘Tęczy’. W omawianym roku stwierdzono, że średni procent uszkodzonej powierzchni liści w całym okresie wegetacji istotnie najwyższy był na ‘Polanowskiej’ w porównaniu z wszystkimi odmianami oprócz ‘Tęczy’. Z kolei najbardziej odporną na żerowanie wciornastków była ‘Wenta’.

W 2016 roku, w początkowym okresie wegetacji roślin, istotnie najliczniej zasiedlane przez migrujące wciornastki były ‘Alibaba’, ‘Kristine’, ‘Niagara F₁’ oraz ‘Polanowska’, natomiast najmniej licznie zasiedlane były ‘Bila’ i ‘Tęcza’. W całym sezonie wegetacyjnym istotnie najwyższą średnią liczbę imago i larw wciornastków zebrano z ‘Alibaby’ i ‘Niagary F₁’, podczas gdy istotnie najmniejszą z ‘Tęczy’. Średni procent uszkodzonej przez żerujące wciornastki powierzchni liści był istotnie najwyższy na ‘Karmen’, ‘Kristine’ i ‘Polanowskiej’, natomiast najniższy na ‘Wencie’.

W obydwu latach badań stwierdzono istotnie wyższą średnią liczbę larw wciornastków zebranych w całym sezonie wegetacyjnym na odmianach 'Alibaba' i 'Niagara F₁' w porównaniu z wszystkimi pozostałymi odmianami.

Analiza statystyczna wykazała istotne różnice w średniej liczbie larw i dorosłych wciornastków zebranych z odmian cebuli w większości terminów pobierania prób, natomiast tylko w niektórych, w przypadku procentu uszkodzonej powierzchni liści. W 2015 roku na początku lipca zagęszczenie tych szkodników było istotnie mniejsze na odmianach 'Tęcza', 'Alibaba' i 'Wenta' w porównaniu z resztą testowanych odmian. W lipcu i sierpniu liczebność wciornastków była na ogół istotnie niższa na odmianach 'Kristine', 'Tęcza' i 'Wenta'. Z kolei w sezonie wegetacyjnym 2016 roku, populacja wciornastka tytoniowca była z reguły wyższa na odmianach 'Alibaba', 'Niagara F₁' i 'Polanowska' w porównaniu do odmian 'Bila', 'Karmen' i 'Tęcza'. W 2015 roku w większości terminów najbardziej uszkodzona przez wciornastki była 'Polanowska' i 'Tęcza', a najmniej 'Wenta'. Z kolei w 2016 jedynie 7 lipca istotnie najbardziej uszkodzone były liście odmiany 'Tęcza', a w dwóch ostatnich terminach pobierania prób tj. w sierpniu, istotnie najbardziej uszkodzonymi odmianami były 'Karmen' i 'Polanowska', podczas gdy najmniej uszkodzone były 'Alibaba' i 'Wenta'.

Na podstawie uzyskanych wyników oraz przyjętej skali uznano, że odmiana 'Wenta' jest umiarkowanie odporna na rozwój wciornastka tytoniowca oraz odporna na jego żerowanie. Również odporna na rozwój wciornastków była odmiana 'Tęcza', niestety odmiana ta była podatna na żerowanie tych szkodników. Pozostałe sześć odmian, tj.: 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁' i 'Polanowska', stwarzały dobre warunki dla rozwoju i żerowania wciornastka tytoniowca i zostały uznane za podatne, przy czym 'Niagara F₁' była wysoce podatna na rozwój, a 'Polanowska' na żerowanie wciornastków. Wszystkie podatne odmiany były również najbardziej atrakcyjne dla migrujących dorosłych osobników wciornastka tytoniowca w początkowym okresie zasiedlania roślin, przy czym najbardziej atrakcyjna w tym czasie była odmiana 'Niagara F₁'. Odmiana 'Tęcza' była odporna, a odmiana 'Wenta' była średnio odporna na zasiedlenie przez kolonizujące je wciornastki.

Równoległe do badań polowych przeprowadzono analizy biochemiczne w celu ustalenia czy zawartość cukrów rozpuszczalnych, cukrów redukujących, sacharozy i fenoli ogółem może mieć wpływ na odporność odmian na rozwój i żerowanie wciornastka tytoniowca.

Zarówno w 2015, jak i 2016 roku stwierdzono statystycznie istotny wpływ odmiany cebuli na zawartość wyżej wymienionych składników w liściach cebuli (nieuszkodzonych przez żerujące wciornastki).

W 2015 roku większość odmian cebuli różniła się istotnie od siebie pod względem zawartości cukrów rozpuszczalnych i sacharozy w liściach, a jedynie pomiędzy odmianami 'Karmen' i 'Niagara F₁' oraz 'Bila' i 'Kristine' nie stwierdzono istotnych różnic. Największą średnią zawartością cukrów rozpuszczalnych i sacharozy w liściach charakteryzowała się odporna na żerowanie wciornastków 'Wenta'. Z kolei najmniejszą zawartością obu węglowodanów wyróżniała się 'Polanowska', która była podatna i stwarzała dogodne warunki do rozwoju i żerowania wciornastków. W omawianym roku, w liściach odmian cebuli najbardziej zasiedlonych, ale umiarkowanie uszkodzonych przez wciornastki jak 'Alibaba' oraz 'Niagara F₁', stwierdzono istotnie największą zawartość cukrów redukujących. Podatna na uszkodzenia wciornastków odmiana 'Kristine' zawierała najmniej cukrów redukujących. W 2015 roku odporna na rozwój i żerowanie wciornastków 'Wenta' charakteryzowała się najwyższą średnią zawartością fenoli ogółem. Odmiany 'Alibaba' i 'Niagara F₁' należały odpowiednio do drugiej i trzeciej grupy jednorodnej, podczas gdy pięć pozostałych odmian tworzyło czwartą grupę, w której najmniej fenoli ogółem zawierały liście odmiany 'Kristine'.

W 2016 roku, w przeciwieństwie do roku poprzedniego, liście najbardziej podatnej na rozwój i żerowanie wciornastków, odmiany 'Polanowska', zawierały najwięcej cukrów rozpuszczalnych i sacharozy. Z kolei najniższą zawartość tych węglowodanów posiadały odmiany również podatne na żerowanie wciornastków tj. 'Bila' i 'Kristine'. Najwyższy poziom zawartości cukrów redukujących zawierały liście podatnej na rozwój wciornastków 'Alibaby', a następnie dwie podatne zarówno na rozwój, jaki i żerowanie wciornastków odmiany 'Niagara F₁' i 'Polanowska'. Przeciwnie, najmniej cukrów redukujących stwierdzono w liściach odmiany 'Wenta', która była odporna na żerowanie szkodników. W 2016 roku istotnie najwyższą zawartość fenoli stwierdzono w liściach 'Tęczy', 'Alibaby' i 'Wenty'. Odmiany te charakteryzowały się odpowiednio wysokim, średnim i niskim stopniem uszkodzenia liści w omawianym roku. Najniższe zawartości tych związków biochemicznych wykryto w liściach odmian podatnych na żerowanie wciornastków, tj. 'Bila', 'Kristine' i 'Polanowska'.

W 2015 roku zawartość cukrów redukujących w nieuszkodzonych liściach odmian cebuli była istotnie dodatnio skorelowana ze średnią liczbą wciornastków w dniu 28 lipca (kiedy pobrano próbki liści do analiz biochemicznych) oraz ze średnią liczbą wciornastków zebraną w ciągu całego sezonu wegetacyjnego. Z kolei zawartości cukrów rozpuszczalnych

ogółem, sacharozy i fenoli ogółem korelowały istotnie ujemnie ze średnim sezonowym procentem uszkodzonej powierzchni liści.

W roku 2016 współczynnik korelacji wskazał na istotnie dodatnią zależność między zawartością wszystkich trzech cukrów a średnią liczbą wciornastków zebranych z roślin 8 sierpnia (kiedy pobrano próbki liści do analiz biochemicznych) oraz między zawartością cukrów redukujących a średnią liczbą wciornastków w całym sezonie wegetacyjnym cebuli. Stwierdzono natomiast istotną ujemną korelację między zawartością fenoli ogółem a średnim procentem uszkodzonej powierzchni liści w dniu 8 sierpnia, a także w całym sezonie wegetacyjnym.

W 2016 roku zbadano również wpływ wybranych cech anatomicznej budowy liści testowanych odmian cebuli na ich odporność na rozwój i żerowanie wciornastków. Grubość blaszki liściowej u testowanych odmian była cechą istotnie zróżnicowaną. Stwierdzono, że najgrubsze blaszki liściowe posiadały liście 'Alibaby' i 'Karmen', natomiast najcieńsze blaszki liściowe miała 'Polanowska' i tuż za nią 'Wenta'. W przypadku epidermy istotnie najgrubszą jej warstwę miały liście 'Kristine' w porównaniu z pozostałymi odmianami, z wyjątkiem dwóch 'Bili' i 'Karmen'. Z kolei najcieńszą warstwę epidermy posiadała 'Wenta', jednak nie różniła się ona istotnie od grubości epidermy w liściach: 'Alibaby', 'Niagary F₁', 'Polanowskiej' i 'Tęczy'. Komórki epidermy liści 'Alibaby', 'Karmen' i 'Wenty' miały istotnie mniejszy obwód oraz powierzchnię w porównaniu z 'Kristine' i 'Polanowską'. Odmiana 'Alibaba' posiadała także mniejsze komórki mezofilu w porównaniu z innymi odmianami cebuli. Ich obwód i powierzchnia okazały się istotnie mniejsze w porównaniu do pozostałych odmian cebuli, z wyjątkiem powierzchni komórek mezofilu odmiany 'Polanowska'. Liście wszystkich odmian cebuli miały podobną liczbę warstw komórkowych w mezofilu (około 6-8 warstw). Wiązki naczyniowe u wszystkich odmian były ułożone w jednym rzędzie. Stwierdzono istotny wpływ odmiany jedynie na średnią odległość między wiązkami naczyniowymi pomiędzy testowanymi odmianami. Najbardziej oddalone od siebie były wiązki naczyniowe 'Alibaby' w porównaniu z innymi, oprócz 'Bili' i 'Karmen'. Natomiast istotnie najbliżej siebie położone były wiązki naczyniowe odmiany 'Polanowska' w porównaniu do pozostałych, z wyjątkiem: 'Kristine', 'Niagary F₁', 'Tęczy' oraz 'Wenty'. Pomimo braku istotnych różnic pomiędzy średnią wartością średnicy, obwodu i pola przekroju poprzecznego wiązek naczyniowych badanych odmian cebuli, najmniejszy średni obwód i średnie pole przekroju poprzecznego stwierdzono w liściach odmiany 'Wenta', która była najmniej uszkodzona przez wciornastki

w 2016 roku. Natomiast wymienione parametry miały największą wartość u odmian 'Bila' i 'Karmen', które były silnie uszkodzone przez te szkodniki.

Współczynnik korelacji parametrów anatomicznych liści cebuli wykazał istotną zależność pomiędzy trzema zmiennymi. Średnia powierzchnia komórek mezofilu korelowała ujemnie ze średnią liczbą wciornastków z całego sezonu wegetacyjnego, podobnie jak średni obwód wiązek naczyniowych ze średnią liczbą wciornastków zebranych z liści 8 sierpnia (w dniu, kiedy pobierano liście cebuli do badań anatomicznych) oraz w całym sezonie wegetacyjnym. Odwrotnie, średnia powierzchnia komórek mezofilu była dodatnio skorelowana z procentem uszkodzonej powierzchni liścia odnotowanym w dniu 8 sierpnia.

W publikacji tej przedstawiono również wyniki badań nad wpływem żerowania wciornastka tytoniowca na zawartość cukrów rozpuszczalnych, redukujących i sacharozy, związków fenolowych ogółem oraz barwników roślinnych, takich jak chlorofili a i b, karotenoidów ogółem w uszkodzonych liściach badanych odmian cebuli.

Największy spadek zawartości cukrów rozpuszczalnych i sacharozy (> 20,0%) odnotowano u odmian 'Alibaba', 'Karmen' i 'Wenta' w 2015 oraz 'Kristine' i 'Niagara F₁' w 2016 roku, natomiast najmniejszy (< 10,3%) u odmiany 'Bila' i 'Kristine' w 2015 roku. Ponadto wyraźny spadek zawartości sacharozy (> 20,0%) zaobserwowano również w uszkodzonych liściach odmiany 'Polanowska' i 'Niagara F₁' w 2015 roku. W 2015 roku, żerowanie wciornastków na odmianach 'Alibaba', 'Karmen' i 'Niagara F₁' nie wpłynęło istotnie na zmniejszenie zawartości cukrów redukujących, natomiast spowodowało istotny wzrost zawartości tych cukrów w uszkodzonych liściach odmiany 'Wenta' (> 50,0%) oraz 'Bila', 'Tęcza', 'Kristine' i 'Polanowska' (od 15,33% do 25,56%). Również w 2016 roku, odmiana 'Tęcza' odpowiedziała na żerowanie wciornastków istotnym wzrostem zawartości cukrów redukujących, natomiast w przypadku odmian 'Bila' i 'Wenta' odnotowano reakcję odwrotną.

W 2015 roku, wszystkie odmiany cebuli zareagowały na żerowanie wciornastków wzrostem zawartości fenoli ogółem powyżej 10,0%, a jedynie u dwóch odmian 'Niagara F₁' i 'Polanowska' wzrost fenoli był niższy niż 10,0%. W 2016 roku, stwierdzono istotny wzrost zawartości fenoli ogółem (> 10,0%) w uszkodzonych liściach odmian: 'Bila', 'Karmen', 'Polanowska', 'Tęcza' i 'Wenta'.

W obydwu latach badań w uszkodzonych liściach wszystkich odmian cebuli stwierdzono spadek zawartości barwników liściowych w porównaniu do liści

nieuszkodzonych. W 2015 roku, istotny spadek zawartości chlorofilu a (od 4,8% do 9,5%) stwierdzono w uszkodzonych liściach pięciu odmian: 'Bila', 'Karmen', 'Kristine', 'Polanowska' i 'Tęcza', natomiast chlorofilu b (od 12,6% do 18,3%) w liściach trzech odmian 'Kristine', 'Niagara F₁' i 'Wenta'. Zawartość karotenoidów istotnie obniżyła się pod wpływem żerowania wciornastków u dwóch odmian 'Bila' (3,7%) i 'Wenta' (5,5%). W 2016 roku stwierdzono istotne obniżenie zawartości chlorofilu a w liściach odmian 'Niagara F₁' (4,5%) i 'Tęcza' (20,0%), chlorofilu b w liściach odmian 'Bila' i 'Karmen' (> 5,0%) i odmianie 'Tęcza' (24,8%) oraz sumy karotenoidów u odmiany 'Niagara F₁' (8,75%) i 'Tęcza' (28,2%).

8. Podsumowanie i wnioski końcowe

1. Cebula zwyczajna (*Allium cepa* L.) i cebula siedmiolatka (*Allium fistulosum* L.) była zasiedlana w okresie wegetacyjnym głównie przez dwa polifagiczne i roślinożerne gatunki wciornastków: wciornastka tytoniowca (*Thrips tabaci* Lind.), wciornastka kwiatowca (*Frankliniella intonsa* Trybom) oraz jeden drapieżny gatunek wciornastka pstrokacza (*Aeolothrips intermedius* Bagnall). Osobniki tych gatunków stanowiły 97% wszystkich wciornastków zebranych z obu gatunków cebuli.
2. Na wszystkich odmianach cebuli zwyczajnej najliczniej występował wciornastek tytoniowiec, a jego udział w zebranych materiale wahał się od 58,7% w 2014 roku do 68,7% w 2015 roku. Drugim pod względem liczby zebranych osobników był wciornastek kwiatowiec z udziałem od 28,5% w 2015 roku do 32,9% w 2014 roku. Udział drapieżnego gatunku wciornastka pstrokacza wahał się od 2,31% w 2015 do 9,13% w 2016 roku.
3. Na cebuli siedmiolatce obserwowaliśmy odwrotną zależność i najliczniejszy był wciornastek kwiatowiec z udziałem 85,6% w 2014 i 59,1% w 2015 roku. Jedynie w 2016 roku jego udział w zebranych materiale wynosił 43,8% i był niższy niż wciornastka tytoniowca, którego udział stanowił 45,5%. Udział wciornastka tytoniowca w latach 2014 i 2015 wynosił odpowiednio 9,45% i 38,1%. Z kolei udział wciornastka pstrokacza wahał się od 0,9% w 2015 roku do 5,75% w 2016 roku.
4. Na wszystkich odmianach cebuli zwyczajnej i siedmiolatki populację wciornastka tytoniowca, wciornastka kwiatowca oraz wciornastka pstrokacza stanowiły głównie samice (> 95,0%). Jedynie w 2016 roku w populacji wciornastka pstrokacza odnotowano występowanie większej liczby samców (79,7%).
5. W czerwcu rośliny cebuli zwyczajnej i siedmiolatki były zasiedlane głównie przez wciornastka tytoniowca oraz wciornastka kwiatowca, jednak z wyższym udziałem wciornastka tytoniowca w zebranych materiale. W pierwszej połowie lipca na odmianach cebuli zwyczajnej nadal utrzymywała się przewaga liczbowa wciornastka tytoniowca nad wciornastkiem kwiatowcem, natomiast na cebuli siedmiolatce populacje obu gatunków były porównywalne lub przewagę miał wciornastek kwiatowiec. Od połowy lipca do końca sierpnia w 2014 roku wciornastek tytoniowiec dominował tylko na niektórych odmianach cebuli zwyczajnej, natomiast w latach 2015-2016 gatunek ten był najliczniejszy na większości jej odmian. Z kolei na cebuli siedmiolatce w latach 2014-2015 w lipcu i sierpniu dominował wciornastek

- kwiatowiec, natomiast w 2016 roku był on dominujący tylko w drugiej połowie lipca i sierpnia. Drapieżny gatunek obserwowany był przez wszystkie lata w lipcu i sierpniu, a jego udział w zebranych materiale wzrastał zwłaszcza w sierpniu.
6. Prowadzone badania potwierdziły, że barwa liści cebuli zwyczajnej może istotnie wpływać na ich atrakcyjność dla migrujących i kolonizujących rośliny dorosłych osobników wciornastka tytoniowca. Spośród ośmiu testowanych odmian wyróżniono dwie odmiany 'Tęcza' i 'Wenta', które były mniej atrakcyjne dla wciornastka tytoniowca podczas wyboru rośliny do zasiedlenia i prawdopodobnie posiadały mechanizm antyksenozę związany z barwą liści. Liście odmian odpornych na zasiedlenie 'Tęczy' i 'Wenty' miały ciemniejsze i zielono-szaro-żółtawe liście w porównaniu do żywej, intensywnej zielono-żółtej barwy liści jaką obserwowano u wszystkich pozostałych i podatnych na zasiedlenie odmian cebuli zwyczajnej.
 7. Stwierdzono, że na podstawie liczby żerujących wciornastków na cebuli nie można przewidzieć stopnia powodowanych przez nie uszkodzeń, chociaż w przypadku wielu testowanych odmian cebuli, większa populacja wciornastków sprzyjała większym uszkodzeniom roślin.
 8. Uznano, że odmiana 'Wenta' była umiarkowanie odporna na rozwój wciornastka tytoniowca oraz odporna na jego żerowanie. Z kolei odporna na rozwój wciornastków odmiana 'Tęcza', niestety była podatna na żerowanie tych szkodników. Pozostałe sześć odmian: 'Alibaba', 'Bila', 'Karmen', 'Kristine', 'Niagara F₁' i 'Polanowska' były podatne zarówno na rozwój, jak i żerowanie wciornastka tytoniowca, przy czym odmiana 'Niagara F₁' była wysoce podatna na rozwój, a odmiana 'Polanowska' na żerowanie wciornastków. Wszystkie podatne odmiany cebuli zwyczajnej na rozwój i żerowanie wciornastków były również podatne na ich zasiedlenie przez migrujące dorosłe wciornastki we wczesnym okresie rozwoju roślin, przy czym najbardziej atrakcyjna była odmiana 'Niagara F₁'. Z kolei odmiana 'Tęcza' była odporna, a odmiana 'Wenta' była średnio odporna na zasiedlenie przez kolonizujące je wciornastki.
 9. Wyniki naszych badań wskazują, że odporność niektórych odmian cebuli zwyczajnej na rozwój i żerowanie wciornastków może mieć związek z mechanizmem antyksenozy i/lub antybiozy, które z kolei mogą być związane z zawartością cukrów i fenoli w liściach odmian odpornych. W obydwu latach badań (2015-2016) udowodniono dodatnią korelację między zawartością cukrów redukujących a liczebnością

wciornastków w całym sezonie wegetacyjnym, oraz ujemną korelację między zawartością fenoli ogółem a procentem uszkodzonej powierzchni liści przez wciornastki. Jedynie w 2015 stwierdzono, że wyższa zawartość cukrów rozpuszczalnych i sacharozy w liściach cebuli była istotnie ujemnie skorelowana z procentem uszkodzonej powierzchni liści cebuli. Ze względu na rozbieżności w wynikach między dwoma latami badań, rola cukrów rozpuszczalnych i sacharozy w odporności roślin na wciornastki musi być interpretowana z ostrożnością. Określenie ilościowego i jakościowego składu cukrów i fenoli w liściach różnych odmian cebuli może ujawnić ich rolę w mechanizmie odporności roślin cebuli na wciornastki i w przyszłości może również przyczynić się do udoskonalenia programów hodowli odpornych odmian cebuli na tego szkodnika.

10. Stwierdzono, że pewne elementy budowy anatomicznej liści cebuli mogą wpływać na rozwój i żerowanie wciornastków. Średnia powierzchnia komórek mezofilu i średni obwód wiązek naczyniowych korelował ujemnie ze średnią liczbą wciornastków zebranych w całym sezonie wegetacyjnym z roślin cebuli. Z kolei średnia powierzchnia komórek mezofilu była dodatnio skorelowana z procentem uszkodzonej powierzchni liścia odnotowanym w dniu wykonania analizy liści.
11. Żerowanie wciornastka tytoniowca wpłynęło na zmniejszenie zawartości cukrów rozpuszczalnych i sacharozy w liściach wszystkich odmian cebuli, jednak istotny spadek wykazano w przypadku odmian 'Alibaba', 'Karmen' i 'Wenta' w 2015 oraz 'Kristine' i 'Niagara F₁' w 2016 roku. Z kolei odmiany: 'Bila', 'Kristine', 'Polanowska', 'Tęcza' i 'Wenta' w 2015 roku oraz 'Tęcza' w 2016 roku, zareagowały na żerowanie wciornastków istotnym wzrostem zawartości cukrów redukujących. Jedynie istotny spadek zawartości cukrów redukujących stwierdzono u odmiany 'Bila' i 'Wenta' w 2016 roku.
12. W 2015 roku, wszystkie odmiany odpowiedziały na żerowanie wciornastków istotnym wzrostem zawartości fenoli ogółem w liściach uszkodzonych przez żerujące wciornastki, natomiast w 2016 roku, istotny wzrost zawartości fenoli ogółem stwierdzono w liściach odmian: 'Bila', 'Karmen', 'Polanowska', 'Tęcza' i 'Wenta'.
13. Żerowanie wciornastka tytoniowca wpłynęło negatywnie na zawartość barwników roślinnych w liściach cebuli zwyczajnej. W obydwu latach stwierdzony istotny spadek zawartości chlorofilu a w liściach wszystkich odmian cebuli zwyczajnej, z wyjątkiem odmian 'Alibaba', 'Niagara F₁' i 'Tęcza' w 2015 roku. Istotny spadek chlorofilu b

stwierdzono w liściach odmian 'Kristine', 'Niagara F1' i 'Wenta' w 2015 roku oraz w liściach wszystkich odmian z wyjątkiem odmiany 'Polanowska' w 2016 roku. Z kolei istotny spadek karotenoidów obserwowano w liściach odmiany 'Bila' i 'Wenta' w 2015 roku oraz w liściach wszystkich odmian w 2016 roku.

14. W związku z powyższym, odmiana 'Wenta', która była odporna na kolonizację, rozwój i żerowanie wciornastka tytoniowca powinna być zalecana producentom cebuli do uprawy. Odmiana 'Wenta' oraz odmiana 'Tęcza' ze względu na jej niską atrakcyjność dla migrujących wciornastków oraz z uwagi na jej odporność na rozwój wciornastków, powinny być dalej badane pod kątem obecności cech, które mogą warunkować ich niższy poziom zasiedlenia i/lub uszkodzenia przez wciornastka tytoniowca.
15. Wytypowano dwie odmiany cebuli zwyczajnej odporne na rozwój wciornastka w czasie całego sezonu wegetacyjnego, 'Tęcza' oraz 'Wenta', a także jedną odmianę, 'Wenta', odporną na ich żerowanie.

Obecnie przygotowywana jest do druku praca, w której zostaną przedstawione wyniki testów biologicznych przeprowadzonych w laboratorium podczas stażu w ramach programu ERASMUS+ na Uniwersytecie Przyrodniczymi (BOKU) w Wiedniu.

9. Literatura

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10. Załączniki – publikacje będące przedmiotem rozprawy doktorskiej

10.1. Publikacja nr 1

Thrips (Thysanoptera) associated with onion (*Allium cepa* L.) and Welsh onion (*Allium fistulosum* L.)

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ABSTRACT

We determined the abundance, species composition, sex ratio and seasonal dynamics of thrips on one cultivar of Welsh onion (*Allium fistulosum*) and eight cultivars of onion (*Allium cepa*) in South Poland within three vegetation seasons (2014–2016). Nine species of Thysanoptera were identified on *A. cepa* and *A. fistulosum*. Irrespective of the onion cultivar, *Thrips tabaci* was the dominant species (64.4% of all collected thrips specimens), while *Frankliniella intonsa* also occurred in high numbers (28.3%). Conversely, Welsh onion was most often inhabited by *F. intonsa* (62.7%), although *T. tabaci* was also numerous (28.3%). The predatory *Aeolothrips intermedius* accounted for 4.5% on *A. cepa* and 2.9% on *A. fistulosum*. In the most numerous species, *T. tabaci*, *F. intonsa* and *A. intermedius* populations were formed mainly by females. The cultivar most colonised by thrips was Kroll of *A. fistulosum*. The tested cultivars of *A. cepa* demonstrated varying degrees of attractiveness to thrips in the subsequent years. The relationship between populations of *T. tabaci*, *F. intonsa* and *A. intermedius* changed in the subsequent months of the growing season. In June, mainly *T. tabaci* and *F. intonsa* occurred on onion plants, while from July, the percentage shares of *F. intonsa* and the predatory *A. intermedius* in the thrips population on many onion cultivars increased. The level of attractiveness of *A. cepa* related to onion thrips, which is reported as a main pest of onion, varies depending on the year and cultivar.

Keywords: *Aeolothrips intermedius*, arrhenotokous, cultivar, *Frankliniella intonsa*, thelytokous, *Thrips tabaci*

INTRODUCTION

Onions have been consumed for thousands of years in various forms in most cultures of the world. They are most commonly used as an aromatic spice and food supplement, but they are also a valuable source of vitamins, minerals, health-promoting substances and essential oils (Dossa et al., 2018). Nowadays, numerous cultivars of onion (*Allium cepa* L.) are cultivated, from the most popular yellow to red and white onions, as well as the more exquisite Welsh onion (*Allium fistulosum* L.). Welsh onion is grown mainly for its chives, although the small bulbs are also edible. The largest producers of *A. cepa* are China, the United States and India, while the production of *A. fistulosum* is centred in Japan, Korea,

China and Taiwan (Ford-Lloyd and Armstrong, 1993). Among the European Union countries, the leaders in the production and export of onion are Spain, the Netherlands and Poland, while Germany and the Ukraine also have a high onion production (Zaremba, 2015). In Poland, the production of onion amounted to 630,000 and 650,000 tonnes in 2014 and 2016, respectively, while in 2015, due to drought, it fell to 585,000 tonnes. In 2017, the onion production amounted to 667,000 tonnes and was higher compared to next year, when it decreased by 15.6% to 563,000 tonnes in 2018 (Statistics Poland, 2020). In addition to abiotic factors (water deficiency and temperature), which have a significant impact on onion

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yield, important biotic factors limiting its production include pests and pathogens (Kalbarczyk et al., 2011).

Among the onion pests, one of the most harmful ones is the *Thrips tabaci*. Larvae and adults of onion thrips live in the leaf sheath and stalk, sucking up the contents of plant cells and causing direct damage, which manifests in the silvering of the leaves and, consequently, inhibited plant growth and reduced bulb weight. In addition, it has indirect effects by promoting the development of fungal and bacterial pathogens as well as the transmission of Iris yellow spot virus (IYSV) (Lewis, 1973). Furthermore, the rapid mass appearance and the high density of thrips on onion crops, particularly during the hot and dry growing seasons, are associated with serious yield loss (Diaz-Montano et al., 2011; Gill et al., 2015). Fournier et al. (1995) demonstrated that in the absence of any control measures, onion thrips infestations of yellow onions resulted in yield losses of 34.5% and 43%. Similarly, Pandey et al. (2011) reported that onion thrips damaged 90% of the onion crop in India and >50% in the United States (Boateng, 2012). It is also one of the major limiting factors affecting yields of leek (Kucharczyk and Legutowska, 2002), cabbage (Fail and Péntzes, 2004; Trdan et al., 2008a), tomato, pepper, cucumber (Riefler and Koschier, 2009; Ssemwogerere et al., 2013) and peas (Pobożniak et al., 2020). The high potential for a rapid population increase of *T. tabaci* on onion crops is because of a result of their complex lifestyle with a high reproductive rate, a short generation time, a high survival of non-feeding instars (prepupa and pupa), the ability to reproduce without mating (parthenogenesis) and their ability to develop resistance to insecticides (Morse and Hoddle, 2006; Diaz-Montano et al., 2011). Onion thrips do not comprise a homogeneous species and are composed of two distinct reproductive modes: thelytokous and arrhenotokous populations (Nault et al., 2006). The number of generations per year depends on the climatic conditions. In cold areas, from two to three generations may be produced, while in warmer regions, their number can increase up to eight (Gill et al., 2015).

Besides the above-mentioned harmful species *T. tabaci*, other phytophagous thrips taxa arising from neighbouring crops and wild plants can colonise onion plants. Most of them are not known to cause crop damage (Pobożniak et al., 2007), but their presence on onion plants and sticky traps, which are a useful tool for monitoring onion thrips infestation, can be misleading for farmers. Many authors also observed the presence of *Aeolothrips intermedius* on onion crops (Pobożniak et al., 2007; Mautino et al., 2014; Pobożniak et al., 2016), and this predatory taxa reduces the densities of other thrips populations and is a predator of 44 species of the Thysanoptera order (Riudavetes, 1995), potentially controlling onion thrips (Trdan et al., 2005). Accurate identification of thrips pests is fundamental to their effective control. Knowledge of this insect pest biology and seasonal dynamics would allow establishing control strategies in a future Integrated Pest Management (IPM) programme.

In this context, this study aimed to determine thrips abundance, species composition and seasonal fluctuation on eight cultivars of *A. cepa* and one cultivar of *A. fistulosum*. We also assessed the entity of the autochthonous predator *A. intermedius*, which is a potential biological control agent of *T. tabaci*.

MATERIALS AND METHODS

Field and laboratory research on the determination of composition, abundance and significance of particular thrips species was conducted in the Department of Botany, Physiology and Plant Protection of the University of Agriculture in Krakow, Poland.

Plant material

All onion cultivars of *A. cepa* used in the experiment were obtained from three Polish seed breeding companies: PlantiCo Zielonki in Stare Babice (cv. Alibaba with white bulb, cv. Bila, Kristine, Niagra F₁ with yellow bulb and cv. Wenta with red bulb), Polan in Krakow (cv. Karmen with red and cv. Polanowska with yellow bulb) and Spójnia in Nochowó (cv. Tęcza with yellow bulb). The cultivar Kroll, the only cultivar of the Welsh onion *A. fistulosum* (with white bulb), was obtained from PlantiCo Zielonki in Stare Babice.

Study area

In the years 2014–2016, field experiments were conducted at the Experimental Station of the University of Agriculture in Krakow, located in Mydlniki (near Krakow, southern Poland, 50°04'N, 19°51'E, 207 m above sea level) on a typical brown soil with pH 6.5 and an organic carbon content of 18 g · kg⁻¹. The experiment was established using the method of random blocks in four replications. The size of the experimental plots was 12 m² (3 × 4 m²), with a distance of 1 m between the plots. Seeds were sown (25 kg · ha⁻¹) in rows, 0.3 apart, on 6th April 2014, 10th April 2015 and 6th April 2016. The experimental plots were fertilised according to the Integrated Production recommendations for onions in the field. The plots were kept free of weeds throughout the season. No chemical treatments were carried out on the plots during the experiment, and weeding was performed manually. The crops that surrounded the experimental plot were as follows: potatoes, herbs, red beets, white cabbage, zucchini and pumpkin; additionally, sunflowers and ornamental plants, such as marigold and dahlia, grew in the near surroundings. At a distance of about 0.5 km from the experimental site, cereals and rape were grown.

Entomological analyses

In the three successive years (2014–2016), the period of entomological analyses lasted from the second decade of June to the end of August. In 2014, analyses were performed at intervals of 14 days, while in 2015 and 2016, analyses were performed weekly, between 10:00 am and 3:00 pm on sunny days. Sampling

thrips consisted of two methods: thrips collected with sweeping net and the method composed of plant bagging in plastic bags and then analysis in the laboratory. Thrips landing and spreading on plants were gathered in the net, while the second method allowed collecting of specimens hidden under folded leaves and near the base of the bulb. Thrips were collected from onion leaves using a standard entomological sweeping net (35 cm in diameter). Within each testing plot, 25 sweeps were made, and the sweeping nets and samples were placed individually into plastic bags. In parallel to the sweeping net analysis, 10 randomly selected plants from each plot (40 plants for cultivar) were collected and placed in plastic bags, followed by appropriate labelling. The collected material was transported to the laboratory, where insects were hand-separated using a soft brush and thrips were placed in vials containing 75% ethyl alcohol. Because the species complex of thrips and percentage share from net and direct counting from harvested plants were the same or similar (Tables S1 and S2 in Supplementary Materials), specimens collected by both methods from the same plots and date are shown combined in Tables 1–4 and Figures 1–3.

Identification of thrips species

Microscopic slides were prepared under laboratory conditions according to the technique described by Zawirska (1994). The specimens (adults and immature) were identified to species rank with the use of a microscope, following the keys of Zawirska (1994), Zur Strassen (2003) (adults) and Kucharczyk (2010) (larvae).

Sex ratio

The sex ratio (the percentage of females in a population) was calculated using the standard sex ratio formula as presented below (Vasiliiu-Oromulu, 2002):

$$Sr = f: (m + f) \times 100,$$

where Sr is the sex ratio, f is the number of females (imago) and m is the number of males (imago).

Statistical analysis

Statistical analyses were performed using the Statistica 13 software (Dell Inc. 2016). In the case of lack of normality, the data were normalised with $\log(x + 1)$ transformation. Tables and figures contain untransformed data. One-way analysis of variance (ANOVA; the factor was onion cultivar) was performed for the data, i.e. mean number of thrips. Differentiation of the mean values was determined based on Tukey's HSD (honestly significant difference) test ($p < 0.05$).

RESULTS

Abundance and composition of species

In 2014, during the field study, 3,791 thrips belonging to six species were identified in the collected material from the different onion cultivars (Table 1). A significantly

higher number of thrips was recorded on Welsh onion cv. Kroll (932 individuals) ($F = 3.531$, $p < 0.006$) compared with five other cultivars of onion: Wenta, Alibaba, Karmen, Bila and Niagara F_1 , with 349 to 310 specimens on cv. Wenta and Niagara F_1 , respectively (Table 1).

The most abundant species on Welsh onion (cv. Kroll) was *Frankliniella intonsa* (flower thrips) (86.48%); in turn, *T. tabaci* predominated on onion cultivars. In cultivars of *A. cepa*, thrips accounted for 78.75% (cv. Karmen) to 45.60% (cv. Kristine) of the total number of collected thrips specimens. Of the tested onion cultivars, those most inhabited by onion thrips were cv. Tęcza and Polanowska, while the least colonised cultivar was Kristine. The number of *T. tabaci* infested Welsh onion (cv. Kroll) plants was low and almost 1.8 times smaller than the least populated onion cultivar. The third species in terms of the number of individual thrips collected was the predatory *A. intermedius*. Its share in the collected material ranged from 1.22% on cv. Tęcza to 7.74% on cv. Niagara F_1 ; the other three species *Thrips flavus*, *Haplothrips aculeatus* and *Haplothrips leucantemi* accounted for only 2.48% of the total number of thrips (Table 1).

In 2015, 19,450 individuals, belonging to nine species, were identified (Table 2). The highest number of thrips was found on Welsh onion cv. Kroll (4,536 specimens) in comparison to each onion cultivar ($F = 9.995$, $p < 0.000$). With regard to *A. cepa*, significant differences in the number of collected thrips were found only between cv. Karmen (2,439 individuals) and cv. Polanowska (1,475 individuals) (Table 2). In all the collected material from both *Allium* species, from three (cv. Tęcza) to eight (cv. Bila and Niagara F_1) species of thrips were identified. The most numerous species on all onion cultivars was onion thrips, with a total number of individuals of 10,257 (68.89%), while this taxa was second in terms of the number of individuals collected from Welsh onion (39.26%). The share of *T. tabaci* in the collected material from tested *A. cepa* cultivars was from 64.97% (cv. Tęcza) to 73.77% (cv. Wenta). In 2015, the cultivar most inhabited by onion thrips was the Welsh onion cv. Kroll, followed by the cultivars Karmen and Tęcza, both from *A. cepa*. Similar to the previous year, flower thrips constituted the most abundant taxa registered on cv. Kroll (2,687 specimens), accounting for 59.24% of the collected material from *A. fistulosum*. From all tested cultivars of *A. cepa*, 4,260 specimens of *F. intonsa* were collected, comprising 28.62% of all thrips. The highest percentage share of this species was detected on cv. Tęcza (33.31%) and the smallest was on cv. Wenta (24.27%). Of the species *A. intermedius*, we collected 368 individuals, accounting for 0.88% (cv. Kroll) to 2.88% (cv. Kristine) of the total species. Only 0.49% of the total number of thrips constituted the other six species. In addition to species that had been identified in the previous year, we also registered *Thrips fuscipennis*, *Chirothrips hamatus* and *Haplothrips niger* (Table 2).

Table 1. Species composition of thrips (imago and larvae) collected from *Allium cepa* and *Allium fistulosum* by sweeping net and directly from plants in 2014

Cultivars	N	*Alibaba	*Bila	*Karmen	*Kristine	**Kroll	*Niagara F ₁	*Polanowska	*Tęcza	*Wenta	*Total
<i>Thrips tabaci</i> Lindeman, 1889	N (%)	221 65.38	179 56.65	252 78.75	176 45.60	99 10.62	190 61.29	261 60.70	273 66.59	178 51.00	1,829 48.25
<i>Frankliniella intonsa</i> Trybom, 1895	N (%)	93 27.51	101 31.96	51 15.94	187 48.45	806 86.48	84 27.10	148 34.42	129 31.46	141 40.40	1740 45.90
<i>Aeolothrips intermedius</i> Bagnall, 1934	N (%)	14 4.14	14 4.43	9 2.81	13 3.37	20 2.15	24 7.74	11 2.56	5 1.22	18 5.16	128 3.38
<i>Thrips flavus</i> Schrank, 1776	N (%)	6 1.78	13 4.11	1 0.31	6 1.55	5 0.54	6 1.94	7 1.63	3 0.73	3 0.86	50 1.32
<i>Haplothrips leucantemi</i> Schrank, 1781	N (%)	3 0.89	6 1.90	6 1.88	4 1.04	1 0.11	4 1.29	1 0.23	0 –	5 1.43	30 0.79
<i>Haplothrips aculeatus</i> Fabricius, 1803	N (%)	1 0.30	3 0.95	1 0.31	– 0.00	1 0.11	2 0.65	2 0.47	0 –	4 1.15	14 0.37
Total	N	338	316	320	386	932	310	430	410	349	3,791
Mean (± SE)		84.5 b ± 11.2	79.0 b ± 13.8	80.0 b ± 22.2	96.5 ab ± 8.9	233.a ± 47.4	77.5 b ± 15.1	107.0 ab ± 20.8	102.5 ab ± 19.2	87.2 b ± 17.3	
F											3.531
p											0.006

*Cultivars of *A. cepa*.**Cultivar of *A. fistulosum*.Means marked with different letters are significantly different from each other (multiple Tukey's test $p < 0.05$).

Table 2. Species composition of thrips (imago and larvae) collected from *Allium cepa* and *Allium fistulosum* by sweeping net and directly from plants in 2015.

Onion cultivars	*Alibaba	*Bila	*Karmen	*Kristine	**Kroll	*Niagara F ₁	*Polanowska	*Tezca	*Wenta	Total
<i>Thrips tabaci</i>	N	1,241	1,672	1,157	1,781	1,403	1,024	1,059	1,389	12,038
Lindeman, 1889	(%)	69.68	68.55	66.53	39.26	68.31	69.42	64.97	73.77	61.89
<i>Frankliniella intonsa</i>	N	474	705	523	2687	584	417	543	457	6,947
Trybom, 1895	(%)	26.61	28.91	30.07	59.24	28.43	28.27	33.31	24.27	35.72
<i>Aeolothrips intermedius</i>	N	36	55	50	40	58	29	28	34	368
Bagnall, 1934	(%)	2.02	2.26	2.88	0.88	2.82	1.97	1.72	1.81	1.89
<i>Haplothrips niger</i>	N	6	0	3	12	3	3	0	0	30
Osborn, 1883	(%)	0.34	-	0.17	0.26	0.15	0.20	-	-	0.15
<i>Chirothrips hamatus</i>	N	4	2	3	10	2	1	0	2	26
Trybom, 1895	(%)	0.22	0.08	0.17	0.22	0.10	0.07	-	0.11	0.13
<i>Thrips fuscipennis</i>	N	6	5	2	3	2	0	0	0	18
Haliday, 1836	(%)	0.34	0.21	0.12	0.07	0.10	-	-	-	0.09
<i>Thrips flavus</i>	N	13	0	0	0	1	0	0	0	14
Schrank, 1776	(%)	0.73	-	-	-	0.05	-	-	-	0.07
<i>Haplothrips aculeatus</i>	N	1	0	0	3	1	1	0	1	8
Fabricius, 1803	(%)	0.06	-	-	0.07	0.05	0.07	-	0.05	0.04
<i>Haplothrips leucantemi</i>	N	0	0	1	0	0	0	0	0	1
Schrank, 1781	(%)	-	-	0.06	-	-	-	-	-	0.01
Total	N	1,913	2,439	1,739	4,536	2,054	1,475	1,630	1,883	19,450
Mean (± SE)		478.2 bc ± 52.8	609.7 b ± 45.7	434.7 bc ± 41.4	1134.0 a ± 150.4	513.5 bc ± 44.9	368.7 c ± 23.7	407.5 bc ± 32.1	470.7 b ± 51.3	
F										9.995
p										0.000

*Explanations: see Table 1.

Table 3. Species composition of thrips (imago and larvae) collected from *Allium cepa* and *Allium fistulosum* by sweeping net and directly from plants in 2016.

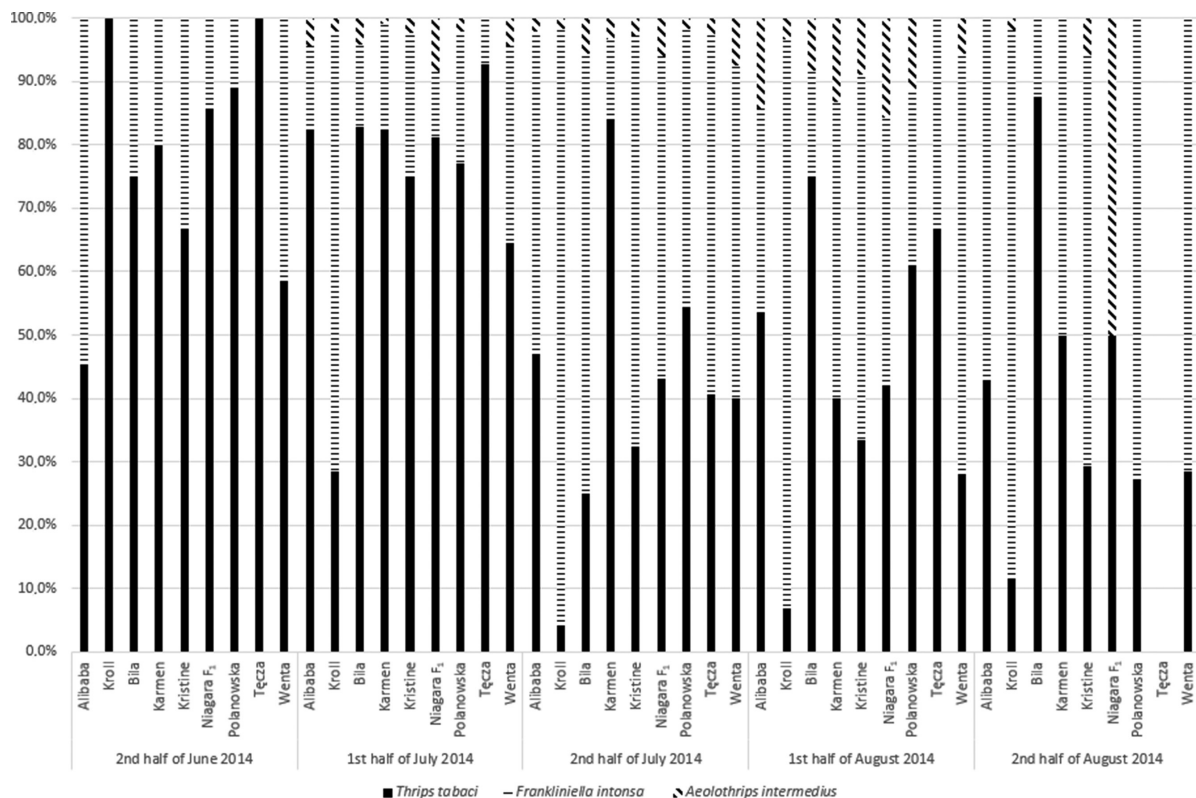
Onion cultivars	*Alibaba	*Bila	*Karmen	*Kristine	**Kroll	*Niagara F ₁	*Polanowska	*Tęcza	*Wenta	Total
<i>Thrips tabaci</i> Lindeman, 1889	N 723 (%) 58.92	494 64.74	578 64.22	639 63.77	1,084 44.10	579 64.12	848 69.28	232 80.28	616 58.17	5,793 58.96
<i>Frankliniella intonsa</i> Trybom, 1895	N 320 (%) 26.08	177 23.20	207 23.00	240 23.95	1043 42.43	214 23.70	247 20.18	29 10.03	298 28.14	2,775 28.24
<i>Aeolothrips intermedius</i> Bagnall, 1934	N 137 (%) 11.17	68 8.91	86 9.56	101 10.08	137 5.57	88 9.75	84 6.86	28 9.69	94 8.88	823 8.38
<i>Haplothrips aculeatus</i> Fabricius, 1803	N 9 (%) 0.73	4 0.52	12 1.33	8 0.80	77 3.13	6 0.66	12 0.98	0 -	13 1.23	141 1.44
<i>Thrips fuscipennis</i> Haliday, 1836	N 10 (%) 0.81	4 0.52	11 1.22	8 0.80	74 3.01	6 0.66	9 0.74	0 -	12 1.13	134 1.36
<i>Chirothrips hamatus</i> Trybom, 1895	N 22 (%) 1.79	9 1.18	4 0.44	1 0.10	23 0.94	7 0.78	20 1.63	0 -	12 1.13	98 1.00
<i>Chirothrips manicatus</i> Haliday, 1836	N 4 (%) 0.33	6 0.79	1 0.11	4 0.40	14 0.57	3 0.33	1 0.08	0 -	10 0.94	43 0.44
<i>Haplothrips leucantemi</i> Schrank, 1781	N 2 (%) 0.16	0 -	1 0.11	1 0.10	5 0.20	0 -	3 0.25	0 -	4 0.38	16 0.16
<i>Thrips flavus</i> Schrank, 1776	N 0 (%) -	1 0.13	0 -	0 -	1 0.04	0 -	0 -	0 -	0 -	2 0.02
Total	N 1,227	763	900	1,002	2,458	903	1,224	289	1,059	9,825
Mean (± SE)	306.7 b ± 21.2	160.7 b ± 15.3	225.0 b ± 29.4	250.5 b ± 42.1	614.5 a ± 55.6	225.7 b ± 28.0	306.0 b ± 20.7	72.2 c ± 15.2	264.7 b ± 29.0	
F										21.671
p										0.000

*Explanations: see Table 1.

Table 4. Sex ratio index of the most numerous species of thrips (imago) collected from *Allium cepa* and *Allium fistulosum* by sweeping net and directly from plants in 2015 and 2016.

Onion cultivars	<i>Thrips tabaci</i>			<i>Aeolothrips intermedius</i>			<i>Frankliniella intonsa</i>		
	Male	Female	Sex ratio	Male	Female	Sex ratio	Male	Female	Sex ratio
2015									
Alibaba	1	1,311	99.9	1	37	97.4	15	542	97.3
Bila	14	1,227	98.9	0	36	100.0	11	463	97.7
Karmen	20	1,652	98.8	4	51	92.7	15	690	97.9
Kristine	2	1,155	99.8	0	50	100.0	12	511	97.7
Kroll**	12	1,769	99.3	5	35	87.5	81	2606	97.0
Niagara F ₁	15	1,388	98.9	0	58	100.0	21	563	96.4
Polanowska	0	1,024	100.0	2	27	93.1	14	403	96.6
Teęcza	0	1,059	100.0	0	28	100.0	0	543	100.0
Wenta	0	1,389	100.0	3	31	91.2	5	452	98.9
2016									
Alibaba	0	723	100.0	33	104	75.9	3	317	99.1
Bila	0	494	100.0	18	50	73.5	2	175	98.9
Karmen	1	577	99.8	18	68	79.1	1	206	99.5
Kristine	1	638	99.8	22	79	78.2	2	238	99.2
Kroll**	0	1,084	100.0	21	116	84.7	21	1,022	98.0
Niagara F ₁	1	578	99.8	25	63	71.6	0	214	100.0
Polanowska	2	846	99.8	18	66	78.6	1	246	99.6
Teęcza	0	232	100.0	0	28	100.0	0	29	100.0
Wenta	0	616	100.0	23	71	75.5	7	291	97.7

**Cultivar of *A. fistulosum*, other cultivars are the *A. cepa*.

**Figure 1.** Share of the three most abundant species on *Allium cepa* and *Allium fistulosum* in 2014 (cv. Kroll – *A. fistulosum*, others cvs – *A. cepa*).

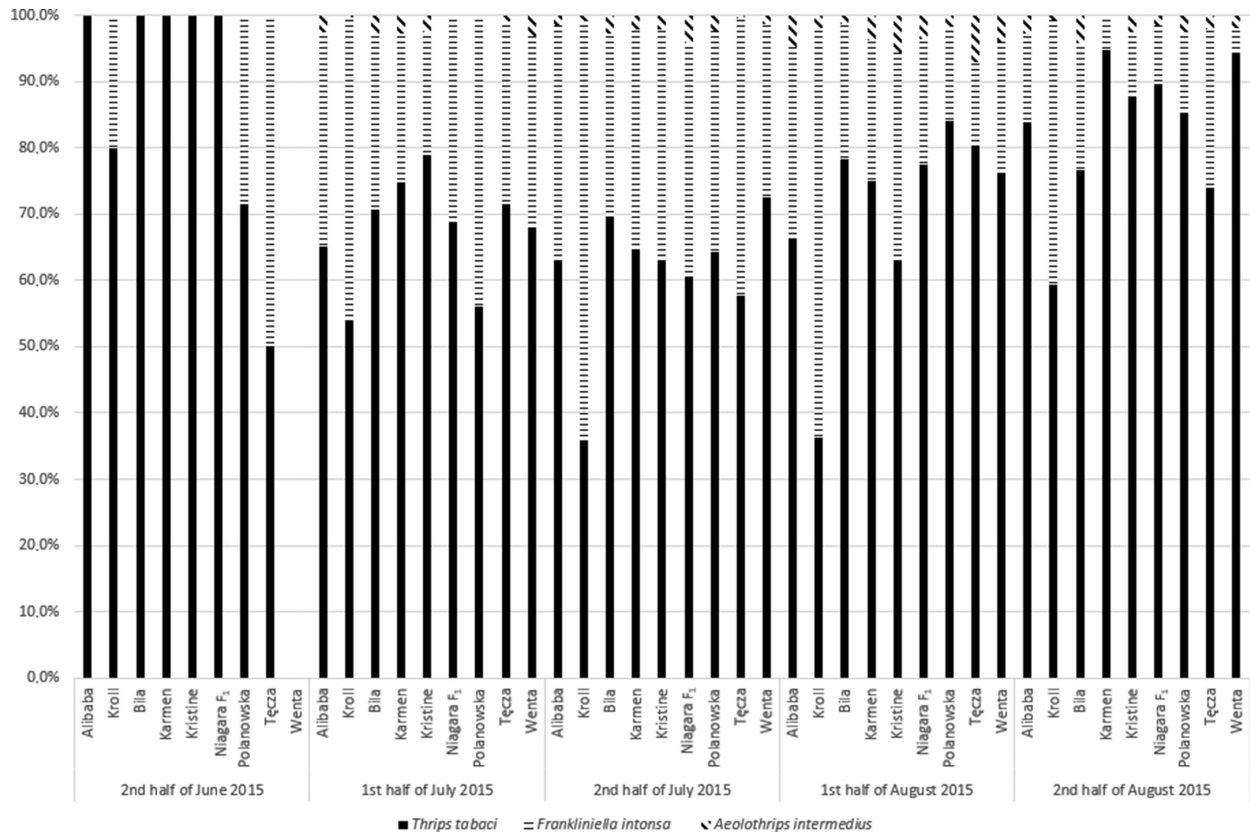


Figure 2. Share of the three most abundant species on *Allium cepa* and *Allium fistulosum* in 2015 (cv. Kroll – *A. fistulosum*, others cvs – *A. cepa*).

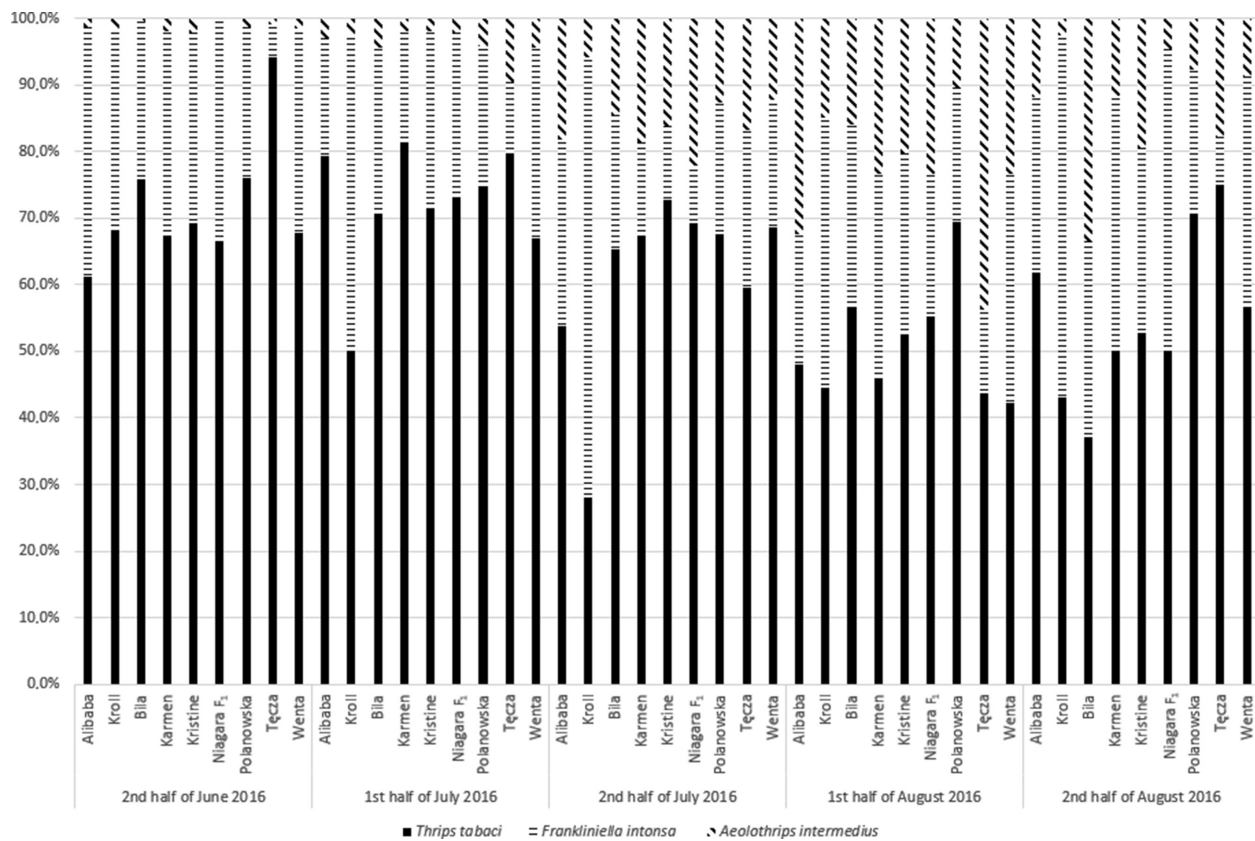


Figure 3. Share of the three most abundant species on *Allium cepa* and *Allium fistulosum* in 2016 (cv. Kroll – *A. fistulosum*, others cvs – *A. cepa*).

In 2016, a total of 9,825 individuals of thrips, belonging to nine species, inhabited Welsh onion and onion plants. The highest number of thrips was found on the Welsh onion cv. Kroll (2,458 specimens) ($F = 21.671$, $p < 0.000$; Table 3), while the lowest number of thrips was observed on the onion cv. Tęcza (289 individuals). Among the cultivars of *A. cepa*, thrips were most abundant on the cultivars Alibaba (1,227 specimens) and Polanowska (1,224 thrips) (Table 3). Irrespective of the number of thrips individuals collected from cultivars of *A. cepa*, the number of detected thrips species ranged from seven to eight, except for cv. Tęcza, where only three species were noted. The insects collected from cv. Kroll represented nine thrips species. The most abundant species on all tested onion cultivars and Welsh onion was onion thrips, with a total number of 5,793 individuals (58.96%). Its share on *A. cepa* cultivars ranged from 58.17% on cv. Wenta to 80.28% on cv. Tęcza, while on cv. Kroll, it reached 44.10%. Of the onion cultivars, the most inhabited one was cv. Polanowska, while the least was cv. Tęcza. The second most abundant species was *F. intonsa* with 2,775 specimens, accounting for 28.24%. Its percentage share was the highest on cv. Kroll (42.43%), while on the other cultivars, it did not exceed 28.14% (cv. Wenta). The third highest percentage share in terms of the number of individual thrips collected in 2016 was found for *A. intermedius* with 823 individuals, accounting for 8.38% (from 5.57% on cv. Kroll to 11.17% on cv. Alibaba). Similar to the previous years, the other six species only accounted for 4.42% of the total species (Table 3).

The comparisons of thrips complex and percentage share of species caught by both sampling methods are presented in Tables 1 and 2. Within 3 years (2014–2016), much more specimens were collected directly from sweeping (18,228 specimens from onion and 6,814 from Welsh onion) than during a direct counting of specimens from harvested plants (respectively, 6,898 and 1,126 specimens from onion and Welsh onion). The complex of dominant species gathered with net and directly from onion and Welsh onion plants was the same and there were little differences between both the methods in the case of accessory species in 2015 and 2016. In 2014, the share of *T. tabaci* caught with sweeping was greater than that collected by direct counting thrips from onion and Welsh onion plants, while in the next 2 years the opposite ratio was noticed in the total collection of sampled thrips from onion and in 2015 from Welsh onion. The share of *F. intonsa* and *A. intermedius* was higher in material collected by direct counting thrips from onion in 2014, while in the next 2 years it was higher in the material gathered in net. In material collected from Welsh onion, the share of *F. intonsa* in net was higher within 2014 and 2015, while the ratio of *A. intermedius* was higher in net only in 2015. In turn in 2016, the share of three dominated species was nearly the same in material gathered by both methods from Welsh onion.

Sex ratio index of the most abundant three species

The population of *T. tabaci* was mainly represented by females. In 2015, 64 males were collected from five cultivars of onion (cv. Alibaba, Bila, Karmen, Kristine and Niagara F₁) and from Welsh onion (cv. Kroll). The numbers ranged from 1 specimen on cv. Alibaba to 20 thrips on cv. Karmen. The calculated sex ratio collected from these cultivars ranged from 98.8% (cv. Karmen) to 99.9% (cv. Alibaba). In 2016, only single males were found on cv. Karmen, Kristine, Niagara F₁ and Polanowska, and the sex ratio was 99.8% in all cultivars (Table 4).

In the population of *F. intonsa*, males occurred in greater numbers. In both years of research, males were registered on all tested cultivars except only on cv. Niagara F₁ in 2016 and Tęcza in both years. Larger numbers of *F. intonsa* males (174 specimens) were caught in 2015, when the overall abundance of thrips was high. In 2016, we registered only 37 males of flower thrips. In both years, most males were caught from *A. fistulosum* (cv. Kroll), which was the cultivar most infested by this species. Its sex ratio on this cultivar was 97% in 2015 and 98% in 2016. On cultivars of *A. cepa*, the sex ratio of *F. intonsa* was similar on all cultivars and ranged from 96.4% to 98.9% in 2015 and from 97.7% to 99.6% in 2016 (Table 4).

In contrast to *T. tabaci* and *F. intonsa*, males of predatory *A. intermedius* were less numerous in 2015, and only single individuals (from two to four) were collected from four cultivars of *A. cepa* (Alibaba, Karmen, Polanowska and Wenta) and five males from cv. Kroll (*A. fistulosum*). Its mean sex ratio on *A. cepa* was 93.6%, while on *A. fistulosum*, it was 87.5% (Table 4). In 2016, from all cultivars infested by *A. intermedius*, 178 males were collected; the mean sex ratio was 76.05% on cultivars of *A. cepa* and 84.7% on cv. Kroll of *A. fistulosum* (Table 4).

Seasonal fluctuation of the most abundant three species

The seasonal fluctuations of *T. tabaci*, *F. intonsa* and *A. intermedius* throughout the three growing seasons (2014–2016) are shown in Figures 1–3.

As shown in Figure 1, in June, among the most numerous species *T. tabaci* and *F. intonsa*, the percentage share of onion thrips on cultivars of *A. cepa* ranged from 45.5% (cv. Alibaba) to 100% (cv. Tęcza). In turn, cv. Kroll (*A. fistulosum*) was at that time only colonised by *T. tabaci*. In the first half of July, *T. tabaci* was the dominant species on all tested cultivars of *A. cepa*, while on *A. fistulosum*, the dominant species was *F. intonsa*, accounting for 69.4%. From mid-July to the end of August, *T. tabaci* accounted for 25.0–87.5% on the onion cultivars, while its share on Welsh onion was low and did not exceed 11.5%. The predatory *A. intermedius* was recorded from the beginning of

June, and its percentage share on all tested cultivars ranged from 1.7% to 15.8%. Only in the second half of August, its share on cv. Niagara F₁ was much higher and amounted to 50.0%.

In June 2015, most of the tested onion cultivars were colonised only by *T. tabaci*, with the exception of cv. Polanowska, Tęcza and Kroll, on which this species accounted for 71.4%, 50.0% and 80.0%, respectively (Figure 2). In July (especially in the second half), the share of *F. intonsa* increased on *A. cepa* from 18.4% (cv. Kristine) to 44.0% (cv. Polanowska) and to 63.5% on *A. fistulosum*. In August, in all cultivars of *A. cepa*, the ratio of the number of both species was reversed, and *T. tabaci* was again the most abundant taxon. On *A. fistulosum*, the share of onion thrips was 36.2% and 59.4%, respectively, in the first and second half of August. Similar to the previous year, *A. intermedius* was caught from the beginning of July to the end of August, mostly from all tested cultivars, and in July, its share in the collected material did not exceed 4.2%, while in August it reached 7.0% (Figure 2).

In June 2016, *T. tabaci* occurred in greater percentages on all tested cultivars (from 61.3% on cv. Alibaba to 94.1% on cv. Tęcza) (Figure 3). This species was also most abundant in July and constituted >50%, except on the cv. Kroll. In August, its percentage share of *A. cepa* ranged from 37.0% (cv. Bila) to 75.0% (cv. Tęcza). The share of *F. intonsa* was the highest on *A. fistulosum*, and in the second half of July, it was as high as 65.9%. From mid-July, an increase in the *A. intermedius* percentage was noticed, with the highest level on the cv. Tęcza in the first half of August (43.8%) (Figure 3).

DISCUSSION

The obtained results indicate that *A. fistulosum* and *A. cepa* plants are colonised by six to nine thrips species throughout the growing season, primarily by the suborder Terebrantia and the family Thripidae. Two herbivorous (*T. tabaci* and *F. intonsa*) and one predatory (*A. intermedius*) species together accounted for over 97% of the material collected from onion and Welsh onion plants throughout 3 years. *T. tabaci* was the most abundant species on all tested cultivars of onion, the second most numerous was *F. intonsa*, while the opposite ratio was noticed on Welsh onion. The participation of thrips species differed by years and both species of *Allium*. The mean share of *T. tabaci* in the total collection of sampled thrips from *A. cepa* ranged from 60.5% to 68.8%, while for *F. intonsa* it was lower and accounted from 23.5% to 32.7%. In turn, in material collected from *A. fistulosum*, the share of onion thrips ranged from 10.6% to 44.1%, while for flower thrips it accounted from 42.4% to 86.4%. Also, Pobożniak et al. (2016) found that the population of *T. tabaci* in onion crops may vary depending on the year, and the share of this species on onions crops can range from 34% to 68%, while for *F. intonsa*, it can range from 29.8% to 58.0%. Onion thrips predominated, accounting for 82.6% to 84.9%

of the thrips on onion in Colorado (USA) (Mahaffey and Cranshaw, 2010). In Texas (USA), according to Bender and Morrison (1989) and Doederlein and Sites (1993), the species composition of thrips on onion is dominated by the western flower thrips (*Frankliniella occidentalis* Pergande) and by onion thrips. Sparks et al. (2011) reported that key arthropod pests on onions in Georgia (USA) are tobacco thrips (*Frankliniella fusca* Hinds), western flower thrips and onion thrips, which represented 49.9% of all detected thrips. The species *T. tabaci* is a major pest and predominant on onion fields in Europe (Hudák and Péntzes, 2004; Diaz–Montano et al., 2011; Gill et al., 2015; Pobożniak et al., 2016), the United States (Macintyre–Allen et al., 2005, Smith et al., 2016), Asia (Pandey et al., 2011; Reitz et al., 2011; Li et al., 2014), Australia (Herron et al., 2008), New Zealand (Martin et al., 2006) and Africa (Maniania et al., 2003). In addition to onion, onion thrips may attack garlic and leek (Afifi and Haydar, 1990; Theunissen and Schelling, 1998; Duchovskienė, 2006; Akhtari et al., 2014) and other vegetables, such as cauliflower, cabbage, pea, cucumber and carrot (Farrugia, 1997; Pourian et al., 2009; Li et al., 2014, Pobożniak et al., 2020; Silva et al., 2020). Notably, the extent and frequency by which onion thrips damage crops vary across plant species, but onion is its preferred host and the most damaged crop. Also, *F. intonsa* has been determined in Poland on the onion by Pobożniak et al. (2016) and on leek by Legutowska and Theunissen (2003). This species is mainly associated with flowering plants and is the dominant species in legume field crops such as peas, beans, soybeans, lentils and lupine in Poland (Pobożniak, 2011; Hurej et al., 2014; 2015). There is no information in the literature on the possibility of *F. intonsa* feeding on onion plants. The author's own observations, however, suggest that this species is not likely to feed on onion, and the presence of *F. intonsa* specimens on onion at least partially may be due to the presence of many flowering plants in the vicinity of the experimental plots. However, Hazir et al. (2011) discussed the possibility of this species feeding on organs other than the flowers. The authors report that *F. intonsa* feeding on ovary tissue caused brown blemishes and scars on nectarine fruit, and feeding on mature fruit caused whitish skin patches called silvering. Also, Murai (1988) noted that swollen white spots were produced as a result of this species feeding on tomato fruits. Moreover, Molnár et al. (2008) observed that in addition to *T. tabaci* and *F. occidentalis* also *F. intonsa* feeds on pepper and can also spread the tomato spotted wilt virus (TSWV) with the same efficacy as the other two species. The very high abundance of *F. intonsa* on onion and the observations of the cited authors indicate a potential possibility of this species feeding also on onions, but this issue requires further clarification.

The predatory *A. intermedius* was a less abundant species and accounting for about 4.5% of all species on *A. cepa* and 2.9% on *A. fistulosum*. Similarly, Pobożniak et al. (2016) found about 5% of *A. intermedius* on *Allium* sp. The appearance of this predatory thrips species

was noticed on *A. fistulosum* in Ljubljana (Trdan et al., 2005). In turn, Ábrahám (2012) observed about 9% of this taxon on alfalfa, and Pobożniak et al. (2020) registered about 8.6% on peas, with the first maximum appearance during the flowering and the second during forming pods phases, when the number of potential victim, onion thrips, was the highest. The occurrence of *A. intermedius* in the flowers of many plants may be due to the fact that pollen can be used as an alternative source of food by this species (Trdan et al., 2005; Conti, 2009). In Europe, *A. intermedius* has usually been mentioned as a predator of onion thrips (Franco et al., 1999). In our experiment, the percentage share of predatory thrips increased on the onion plants from mid-July. In our opinion, *A. intermedius* certainly limited the number of onion thrips on onion plants. However, despite its presence, the numbers of herbivorous onion thrips were so high that they caused damage to the onion leaves. Also, Pobożniak et al. (2020) and Ábrahám (2008) noted that the number of *A. intermedius* was insufficient to reduce the population of phytophagous thrips in pea and soybean. Other species associated with flowers (*Thrips flavus*, *Thrips fuscipennis*, *Haplothrips leucantemi* and *Haplothrips niger*) and mainly with grasses (*Chirothrips hamatus*, *Chirothrips manicatus* and *Haplothrips aculeatus*) were observed on *A. cepa* and *A. fistulosum* in a small numbers. They have also been found in small amounts on onion by Pobożniak et al. (2007), on leek by Legutowska and Theunissen (2003) and on cabbage by Fail and Péntzes (2004) and their presence was accidental and resulted from the neighbourhood of flowering plants and cereals.

The species *T. tabaci* can reproduce asexually (parthenogenesis) and sexually. The most common reproductive mode is thelytoky, a parthenogenesis in which females are produced from unfertilised eggs. Onion thrips also reproduce via arrhenotoky, a parthenogenesis in which males are produced from unfertilised eggs and females from fertilised eggs. Onion thrips that reproduce via thelytoky differ genetically and ecologically from those that reproduce via arrhenotoky (Toda and Murai, 2007). According to Kobayashi et al. (2013), in some instances, arrhenotokous and thelytokous onion thrips populations can coexist in the same field, but it is difficult to distinguish between thelytokous and arrhenotokous female adults morphologically (Jenser and Szénási, 2004). On onion, arrhenotokous *T. tabaci* performed better than thelytokous form and produced more progenies, while on cabbage, the opposite occurred (Li et al., 2014). In our experiment, both females and males of *T. tabaci* were found on *A. cepa* and *A. fistulosum*, and the average sex ratio on all tested onion cultivars was about 99.5% and 99.9% in 2015 and 2016, respectively, and 99.3% and 100% on Welsh onion in subsequent years. Different sex ratios on onions crops, garlic and leeks have also been confirmed by Torres-Vila et al. (1994) in Spain. Both females and males of *T. tabaci* were found also by Bosco and Tavella (2010) on leek under field conditions in northwest Italy. In the Netherlands, the male/female ratio of onion

thrips on leek was 1:26 (Vierbergen and Ester, 2000). In turn, in Ontario (USA), Macintyre-Allen et al. (2005) did not notice the presence of *T. tabaci* males on onion crops. According to Jenser and Szénási (2004), the rare occurrence or absence of male *T. tabaci* is associated with the geographical area from which the host plants originate, including onions and leeks. Their area of origin is Central Asia and the eastern Mediterranean region; *T. tabaci* has been introduced in moderate climate zones, which is likely to explain the absence of males (Jenser and Szénási 2004).

In the case of *F. intonsa*, the average sex ratio on onion cultivars and Welsh onion was nearly the same and accounted for 97.8% and 97.0% on *A. cepa* and 97.0% and 98.0% on *A. fistulosum* in 2015 and 2016, respectively (Table 4). In a population of *F. intonsa* in flowers of food legume plants, participation of males was even higher, with a sex ratio of over 79% Pobożniak (2011). Hurej et al. (2015), in their analysis of thrips settlement on both forms of *Andean lupine*, pointed out that in the case of flower thrips, the morphological form of the plant did not affect the occurrence of male thrips, and the calculated sex ratio was 86.2%.

Mautino et al. (2014) noted that the adult population of *A. intermedius* consists of both female and male zoophages. In our experiment, the sex ratio of this species on *A. cepa* and *A. fistulosum* was about 96.8% and 79.0% on onion and about 87.5% and 84.7% on Welsh onion in 2015 and 2016, respectively (Table 4). Hurej et al. (2017) reported that the sex ratio of *A. intermedius* on linseed ranged from 61.5% to 77.1%, but never exceeded 80%. In turn, on peas, beans, lentil, French beans or soya beans, the percentage of males in the population of *A. intermedius* was lower, and the sex ratio ranged from 82.4% to 89.6% (Pobożniak, 2011).

The relationship between populations of the most numerous species *T. tabaci*, *F. intonsa* and *A. intermedius* changed in the subsequent months of the growing season. In June 2014 and 2015, only *T. tabaci* and *F. intonsa* occurred on onion plants, while in 2016, also a small number of the predatory *A. intermedius* was observed. From July, the percentage shares of *F. intonsa* and predatory *A. intermedius* in the thrips populations on many onion cultivars increased, most likely because of the presence of many flowering plants near the experimental plots and the growing population of *T. tabaci* on onion plants, potential *A. intermedius* prey. Pobożniak et al. (2007; 2016) reported that the peak flight activity of thrips on onion crops in South Poland took place from the beginning of July to the beginning of August and was slightly earlier than that reported for Germany (Richter et al., 1999). In turn, in North Italy, the peak population of onion thrips was reached in September (Bosco and Tavella, 2010), while in South Texas (USA), it peaked in April (Liu, 2004).

Differences in the infestation levels of thrips between the all tested onion cultivars were observed in successive years. In all 3 years of the study, the cultivar most populated by thrips specimens was cv. Kroll (*A. fistulosum*), on which the number of *F. intonsa* was

8 and 1.5 times as high compared to *T. tabaci* in 2014 and 2015, respectively, while the numbers of both species in 2016 were similar. The number of thrips caught from the *A. cepa* cultivars was about from 2 to 3 times lower compared to the thrips population on Welsh onion (cv. Kroll). However, the number of *T. tabaci* on cultivars of *A. cepa* was always higher than that of *F. intonsa*. In the case of some cultivars, the number of *T. tabaci* was even about 3, 5 or 8 times as high compared to *F. intonsa* or was almost the same. In turn, Pobożniak et al. (2016) found that in some years, onion thrips inhabited Welsh onion more frequently compared to onion cultivars. The tested onion cultivars demonstrated varying degrees of attractiveness to thrips species and underwent changes in the subsequent years. The level of attractiveness of onion cultivars related to *T. tabaci*, which is reported as a main pest of onion, varied depending on the year and cultivar. The differences in thrips infestation of the studied cultivars are caused by a number of factors, and clarifying them requires further research. Presumably, factors affecting the colonisation of cultivars by *T. tabaci* were their biochemical and morphological features, influencing the vision, taste and smell senses of thrips, and could be responsible for antixenosis and antibiosis (Smith, 2005; Trdan et al., 2008b; Diaz-Montano et al., 2012; Silva et al., 2014).

CONCLUSIONS

1. In the 3 years of the study, nine species of Thysanoptera were identified on *A. cepa* and *A. fistulosum*. Irrespective of the cultivar of *A. cepa*, *T. tabaci* was the most dominant species, but *F. intonsa* also occurred in high numbers. Conversely, *A. fistulosum* was most often inhabited by *F. intonsa*, although *T. tabaci* was also highly abundant. The predatory *A. intermedius* was among the most numerous species.
2. Of the most numerous species, *T. tabaci* and *F. intonsa*, in each cultivar of *A. cepa* and *A. fistulosum*, populations were formed mainly by females. In the population of *A. intermedius*, males occurred in greater numbers than in the two previously mentioned species.
3. The relationship between populations of the most numerous species *T. tabaci*, *F. intonsa* and *A. intermedius* changed in the subsequent months of the growing season. In June, mainly *T. tabaci* and *F. intonsa* occurred on onion plants, while from July, the percentage shares of *F. intonsa* and the predatory *A. intermedius* in the thrips population on many onion cultivars increased. Throughout the experimental period, the onion cultivar most colonised by thrips was cv. Kroll of *A. fistulosum* in comparison to all tested cultivars of *A. cepa*. The tested cultivars of *A. cepa* demonstrated varying degrees of attractiveness to thrips in the subsequent years.
4. The level of attractiveness of *A. cepa* related to onion thrips, which is reported as a main pest of onion, varies depending on the year and cultivar. The cultivars with higher colonisation rates were Polanowska and Karmen, while the less populated ones were cvs. Tęcza, Bila and Kristine.

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AUTHOR CONTRIBUTIONS

M.O. and M.P. contributed equally to the experimental design, analytical measurements and manuscript writing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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SUPPLEMENTARY MATERIALS

Table S1. Total number and percentage share of thrips species (Thysanoptera) (imago and larvae) collected from *Allium cepa* (mean % for eight tested cultivars) and *Allium fistulosum* (one cultivar) directly from plants in 2014–2016.

Species/year	<i>A. cepa</i>						<i>A. fistulosum</i>		
	2014		2015		2016		2014	2015	2016
	Min–max*	Mean	Min–max	Mean	Min–max	Mean	Mean		
<i>Thrips tabaci</i> Lindeman, 1889	38.24–61.19	51.23	71.96–81.50	78.35	71.53–81.30	76.45	20.11	49.92	40.20
<i>Frankliniella intonsa</i> Trybom, 1895	16.54–41.26	32.17	16.38–25.18	19.84	3.5–20.05	19.36	72.06	49.20	44.64
<i>Aeolothrips intermedius</i> Bagnall, 1934	1.42–19.17	9.69	0.46–2.31	1.49	1.75–3.50	3.73	5.46	0.48	6.14
<i>Chirothrips hamatus</i> Trybom, 1895	–	–	0.00–0.28	0.10	0.00–0.57	0.10	–	0.20	1.11
<i>Chirothrips manicatus</i> Haliday, 1836	–	–	–	–	0.00–0.41	0.07	–	–	0.69
<i>Haplothrips aculeatus</i> Fabricius, 1803	0.00–2.13	1.51	0.00–0.17	0.05	0.00–0.99	0.23	–	–	3.55
<i>Haplothrips leucantemi</i> Schrank, 1781	0.00–3.57	1.41	–	0.03	–	–	0.52	–	0.22
<i>Haplothrips niger</i> Osborn, 1883	–	–	0.00–0.15	–	–	–	–	0.20	–
<i>Thrips flavus</i> Schrank, 1776	0.00–9.75	3.99	–	–	–	–	1.85	–	0.06
<i>Thrips fuscipennis</i> Haliday, 1836	–	–	0.00–0.46	0.14	0.00–0.31	0.06	–	–	3.39
Total number	–	629	–	3999	–	2270	153	659	314

*Min–mean percentage of thrips on onion cultivar with the lowest percentage share; max–mean percentage of thrips on onion cultivar with the highest percentage share.

Table S2. Total number and percentage share of thrips species (Thysanoptera) (imago and larvae) collected from *Allium cepa* (mean% for eight tested cultivars) and *Allium fistulosum* (one cultivar) using sweeping net in 2014–2016.

Species/Year	<i>A. cepa</i>						<i>A. fistulosum</i>		
	2014		2015		2016		2014	2015	2016
	Min–max*	Mean	Min–max	Mean	Min–max	Mean	Mean		
<i>Thrips tabaci</i> Lindeman, 1889	46.63–78.91	63.60	60.58–70.40	65.08	47.54–74.36	60.68	10.69	37.90	40.19
<i>Frankliniella intonsa</i> Trybom, 1895	14.31–49.64	31.58	27.08–37.92	32.04	7.70–17.09	22.09	87.49	60.82	44.63
<i>Aeolothrips intermedius</i> Bagnall, 1934	14.31–49.64	2.44	27.08–37.92	2.36	7.86–17.09	12.85	1.38	1.02	6.69
<i>Chirothrips hamatus</i> Trybom, 1895	–	–	0.10–0.31	0.11	0.00–2.39	1.36	–	0.01	1.01
<i>Chirothrips manicatus</i> Haliday, 1836	–	–	–	–	0.00–1.89	0.64	–	–	0.69
<i>Haplothrips aculeatus</i> Fabricius, 1803	0.00–1.78	0.22	0.00–0.25	0.03	0.00–1.71	1.08	0.13	0.08	3.55
<i>Haplothrips leucantemi</i> Schrank, 1781	0.00–2.40	1.19	–	–	0.00–0.42	0.20	–	–	0.24
<i>Haplothrips niger</i> Osborn, 1883	–	–	0.47–1.02	0.72	–	–	–	0.1	–
<i>Thrips flavus</i> Schrank, 1776	0.31–2.12	0.97	0.00–0.76	0.10	0.00–0.21	0.03	0.31	–	0.06
<i>Thrips fuscipennis</i> Haliday, 1836	–	–	0.00–0.28	0.07	0.00–1.61	1.07	–	0.07	2.23
Total number	–	2230	–	10901	–	5097	779	3891	2144

*Min–mean percentage of thrips on onion cultivar with the lowest percentage share; max–mean percentage of thrips on onion cultivar with the highest percentage share.

10.2. Publikacja nr 2

Article

Relationship between Colonization by Onion Thrips (*Thrips tabaci* Lind.) and Leaf Colour Measures across Eight Onion Cultivars (*Allium cepa* L.)

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Abstract: *Thrips tabaci* Lindeman is a global pest and also represents a serious threat to onion production in Poland. In 2 years (2015–2016) of field studies, 8 onion cultivars were evaluated to characterize their susceptibility to onion thrips and to determine if leaf colour is associated with thrips preference. The actual count and the proportional abundance of adult thrips collected from onion leaves during plant colonization by insects were both used to express the preference of thrips for different onion cultivars. At the same time, the colour measurements were analysed by considering the CIELAB (CIE 1976 L*a*b*) and CIE L*C*h* colour spaces. There were distinct differences in the susceptibility of onion cultivars to colonization by onion thrips. Leaf colour coordinate values were correlated with attractiveness to thrips; typically, higher lightness (L*), yellowness (b*), chroma (C*), hue (h*), and lower redness (a*) attracted more thrips. We concluded that the vivid, intense green-yellowish leaf colour of susceptible varieties might have been the cause of the thrips preference observed. We also identified useful genotypes, Tęcza and Wenta, for host plant resistance to thrips and suggest a link between colour and antixenotic resistance. The resistant cultivars had darker, green-grey-yellowish leaves.

Keywords: antixenosis; CIELAB; CIE L*C*h* colour space; chroma; hue; resistance; yellowness

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1. Introduction

Poland contributes 8.3% of the total onion production in the EU and Polish exports of this vegetable constitute 2.5% of global exports, putting Poland in 9th position in the world [1]. In 2019, onions were cultivated in Poland on an area of 25,200 ha with an average yield of 21.2 t/ha [2]. Onion thrips, *Thrips tabaci* Lindeman 1889 is a global pest [3,4] and also represents a serious threat to onion production in Poland [5]. Larvae and adults of onion thrips live in the leaf sheath and chives, and their feeding causes silvery leaf spots that turn into white blotches along the leaves due to the removal of cellular content. This injury reduces photosynthetic ability and interferes with the transportation of nutrients to the bulb [6]. The negative effects of onion thrips are reflected in both the quantity and quality of the crop [7]. Their feeding causes the reduction of onion bulb mass and also has an indirect effect by creating an entry point for plant pathogens [8,9]. *T. tabaci* is also a vector of Iris yellow spot virus (IYSV) [10]. Effective control of onion thrips necessitates frequent applications of insecticide [11], with the unfortunate result of increased resistance to commonly used chemicals [12,13].

The demand for high-quality onions, produced to the highest standards, is growing continually. For this reason, an increasing number of onion growers are choosing more environmentally friendly methods of cultivation, which allow the use of fewer pesticides.

The choice of a cultivar characterized by a higher degree of resistance to the important pest species for the particular crop is one of the most important agrotechnical measures and an element of integrated pest management (IPM).

Plant characteristics make herbivores prefer one cultivar to another. Some of the plant characteristics are perceivable before landing, such as the size, shape, scent, colour, and light reflectance of the host, while others are perceivable only after landing, such as the physical and chemical parameters of the epidermis or chemical constitution of plant sap [14–16]. Reeves [17] pointed out that despite a general trend of studies and reviews ignoring or downplaying the importance of insect vision in locating host plants in favour of chemical cues, perception of colour and shape can be as important, or in some cases more important, than chemical cues [18,19]. Studies of visual plant characteristics have largely focused on the plant colour, brightness (intensity of perceived reflected light), the polarization of foliar reflectance, saturation (hue clearness), and shape [17,20,21].

Like other insects, thrips use colour, shape, size, and volatiles to locate the host plant. Colour and colour contrast are used by some thrips species to distinguish between a host and the surrounding environment [21]. To determine which colour is most attractive to onion thrips, researchers have tested different colour sticky traps. Behavioural studies of the colour preference of *T. tabaci* have provided variable results, but generally agree that greater numbers of thrips are caught by low UV-reflective white, blue, yellow, and fluorescent yellow traps than are caught by green, red, black, and high UV-reflective white traps [22–27]. According to Demirel and Yeldirim [28], green is regarded as one of the least attractive colours for *T. tabaci*; however, few studies have looked at differences in preference based on a green hue [22,29]. Onion thrips show a significant preference for both light green and mid-green over dark green [29]. Studies on the spectral sensitivity of *T. tabaci* photoreceptors suggest that its vision covers the general insect-visible spectrum between 350 and 650 nm [30]. The last study of Róth et al. [27] indicated that onion thrips possess in their eyes at least two different light receptors: one with peak spectral sensitivity in the greenish-yellow region (540–570 nm) and another in the UV-A region (350–360 nm). Egri et al. [31] established that the spectral sensitivity of the leek-associated biotype L2 of the onion thrips' compound eye has only one striking green peak at 521 nm with only a small shoulder in the UV-A range, while the attractiveness of 350 nm light is much stronger than that of 525 nm for biotype L1 [32].

A mechanism that includes the morphology of a physical plant characteristic by which an insect's behaviour is disturbed, for example, feeding, mating, and oviposition, is known as antixenosis [33]. Antixenosis is an important component of resistance because it reduces the initial infestation level; however, in monoculture, this mechanism may be broken down in the absence of the preferred host plant. In this case, pests may eventually accept a less favoured host [14,15]. Leaf colour has been advocated as an influential factor in determining thrips resistance in onion [34–37]. In recent years, Diaz-Montano [10,38], Fail et al. [39], and Balint et al. [40] have confirmed that antixenosis plays a role in the resistance of onion and white cabbage to onion thrips and also documented that leaf colour and leaf reflectance might positively or negatively influence colonization by *T. tabaci*. The results of Róth et al. [27] suggest that light reflectance in the yellow region and the UV range has the most important effect on the selection of a host plant by *T. tabaci*.

Varietal preference and the susceptibility of onion to *T. tabaci* have been documented in Poland by Pobożniak et al. [41], but no traits were investigated to explain this preference. In this paper, we report the result of measuring the susceptibility of existing commercial onion cultivars to *T. tabaci* infestation concerning leaf colour characteristics. The detailed objectives of the study were to identify cultivars with a high level of nonpreference (antixenosis) that can be cultivated by farmers as a tool of IPM and can also be used by plant breeders as a source of resistance to onion thrips in plant-breeding programmes.

2. Materials and Methods

2.1. Plant Material and Experimental Setup

All of the onion cultivars used in the study are commercially available and were obtained from Polish companies, namely, PlantiCo Zielonki in Stare Babice (cv. Alibaba with a white bulb, cvs. Bila, Kristine, and Niagara F₁ with a yellow bulb and cv. Wenta with a red bulb), Polan in Cracow (cv. Karmen with a red bulb and cv. Polanowska with a yellow bulb) and Spójnia in Nochowo (cv. Tęcza with a yellow bulb). Earlier preliminary screening of a large number of new and F₁ hybrid onion genotypes indicated that the eight genotypes selected might possess resistance or tolerance to the onion thrips [41].

The field experiment was conducted at the Experimental Station of the University of Agriculture in Krakow, located in Mydlniki (near Krakow, in southern Poland, at 50°04'N, 19°51'E and, 207 m above sea level) on a typical brown soil with a pH of 6.5 and an organic carbon content of 18 g/kg. The trial was arranged in a randomized complete block design consisting of four blocks. The plots, measuring 12 m² (3 × 4 m) were separated by 1 m wide paths. The experiment was separated from the neighboring crops (potatoes, herbs, red beets, white cabbage, zucchini, and pumpkin) by a 2 m path. Seeds were sown (25 kg/ha) in rows 0.3 m apart on 10 April 2015 and 6 April 2016. Onion fertilization was in line with integrated production recommendations. No chemical treatments were applied, and weeds were removed from plots and paths mechanically and manually.

2.2. Evaluation of Thrips Abundance

Thrips sampling consisted of two methods: one in which thrips were collected with a sweep net and the second in which plants were bagged into plastic bags. Thrips landing and spreading on plants were gathered in the net, while the second method allowed the collection of specimens hidden under folded leaves and near the base of the bulb. In turn, when harvesting plants, some of the thrips might have flown off them before they were placed in the bags. Within each testing plot, 10 randomly selected plants (40 plants per cultivar) were collected and placed into separate zip-lock plastic bags followed by appropriate labelling. In parallel to this method, thrips were collected from onion leaves using a standard entomological sweep net (35 cm in diameter). Within each testing plot, 25 sweeps were made with the sweep nets, and samples were placed individually into zip-lock plastic bags, followed by appropriate labelling. The collected material was transported to the laboratory, where thrips were hand-separated from the onion plants and sweep net using a soft paint brush (size 1) and placed in vials containing 75% ethyl alcohol (keeping specimens collected directly from plants and with the sweep net separate). Adult individuals of *T. tabaci* were determined to species level according to zur Strassen [42] using a microscopic technique [43].

Based on published data about the effect of temperature on the development of onion thrips [44,45], a degree-day (DD) model was computed for both 2015 and 2016. A single developmental zero temperature (10.3 °C) and a thermal constant (222 DD) for total development (from egg to adult emergence) were calculated. Meteorological data (air temperature and rainfall) were recorded with a HOBO water temperature Pro data logger (Onset Computer Corp., Bourne, MA, U.S.) at hourly intervals at the trial site from May to September in 2015 and 2016. The first adult onion thrips were collected from onion plants on 24 June 2015 and on 16 June 2016. These dates were adopted as the starting point for development of the onion thrips on the tested onion cultivars. From spotting the first adults (starting point), we defined the potential date of appearance of the first adults in the next generation when the heat sum calculation got to 222 DD (Figures 1 and 2). The day for sampling thrips was timed to be well within the calculated 222 DD and took place on 2 July in 2015 and 25 June in 2016.

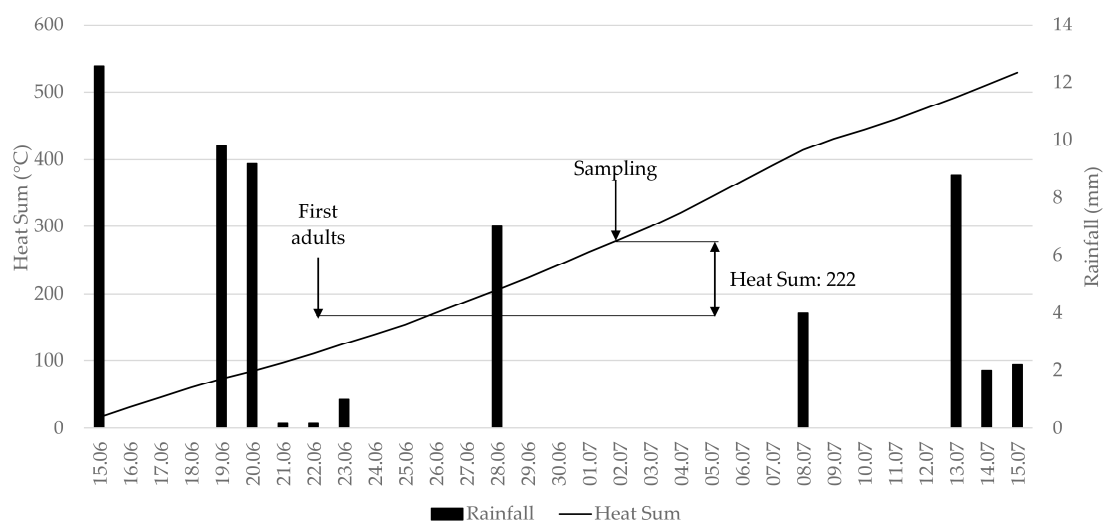


Figure 1. Cumulated effective temperature for the development of *Thrips tabaci* and precipitation recorded in 2015.

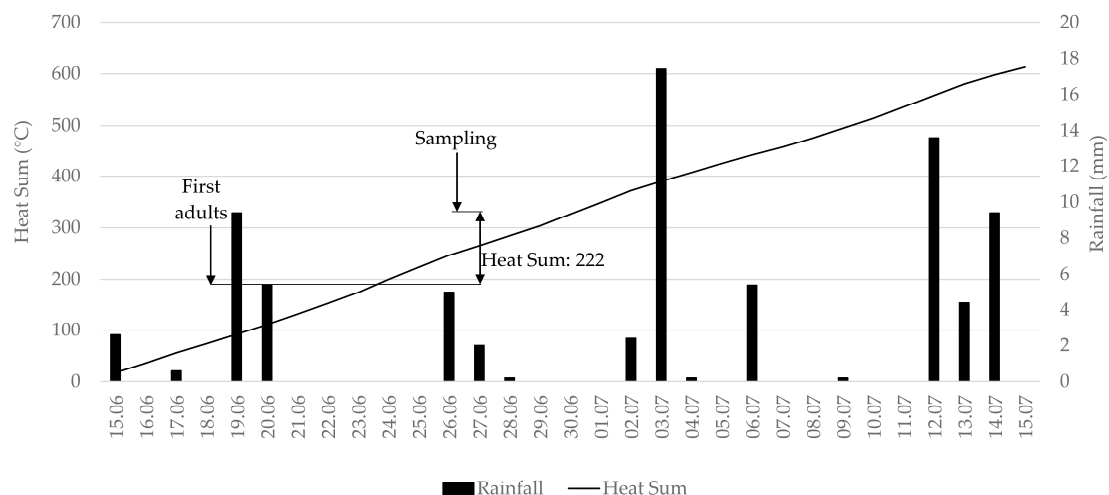


Figure 2. Cumulated effective temperature for the development of *Thrips tabaci* and precipitation recorded in 2016.

The relative proportion of onion thrips (expressed as integer percent values) on each cultivar was computed as a function of the total number of adult *T. tabaci* collected across all eight cultivars. The actual count and the proportional abundance of onion thrips were both used to express the preference of thrips for different onion cultivars and the level of antixenotic resistance of the tested cultivars to this pest.

2.3. Measurement of Leaf Colour

Onion leaf samples for colour measurements were collected consistently for all varieties before sampling of thrips for preference evaluation. The middle leaves from six randomly selected onion plants from each experimental plot were collected and gently wrapped in parchment paper, labelled precisely, and transported to the laboratory. Then, 10 cm sections were cut out of the middle of the leaves very carefully, so as not to damage the wax coating. The sections were placed back into the parchment paper and foil string bags to avoid excessive loss of water and volatile compounds contained in the onion leaves. A total of 192 (6 leaves × 4 blocks × 8 cultivars) sections of onion leaves were prepared for analysis.

The colour was measured with a portable Konica Minolta Chroma Meter spectrophotometer (CM-2600d with 8 mm aperture diffuse illumination and 8 degree (d/8°); Konica Minolta, Inc., Tokyo, Japan) [46], a contact-type colour measuring device commonly used in scientific works [47]. A spectrophotometer is a specific type of spectrometer designed to measure light over the visible and near-ultraviolet portions of the electromagnetic spectrum, i.e., from 360 to 740 nm. Colour measurements were analysed by considering the CIELAB (CIE 1976 L*a*b*) and CIE L*C*h* colour spaces, the most widely accepted by both industry and the scientific community [48–50]. The instrument was calibrated with reference to the white porcelain tile provided by the instrument manufacturer. Each measurement of the object was made from two angles three times, from which the device automatically calculated the average. CIE 1976 L*a*b* is a three-dimensional colour space, where L* represents the lightness; pure white has a full (100%) lightness value, and pure black has no (0%) lightness value. The other colours have intermediate lightness values. Coordinate a* (redness) represents the red to green axis (positive a* is red and negative a* is green), and b* (yellowness) represents the yellow to blue axis (positive b* is yellow and negative b* is blue). Both of them have values between –120 and 120 [48].

Data were also recorded in the CIE L*C*h* colour space, where L* indicates lightness and is the same as L* in the L*a*b* colour space; C* is chroma (an index somewhat analogous to colour saturation or intensity) and may be calculated as the [49]:

$$C_{ab}^* = \sqrt{a^{*2} + b^{*2}}$$

The higher the chroma value, the higher the colour saturation of a sample.

Hue angle (h*) is the colour attribute according to which colours have been traditionally defined as reddish, greenish, etc., and it is used to define the difference of a certain colour from a grey colour with the same lightness. Hue is calculated from the arctangent of b*/a* [49]. Arctangent values assume positive values in the first and third, and negative values in the second and fourth quadrants. For a useful interpretation, h* should remain positive between 0° and 360° of the colour wheel. An angle of 0° or 360° represents a red hue, while angles of 90°, 180°, and 270° represent yellow, green, and blue hues, respectively [49].

The hue difference, ΔH_{ab}^* , between two colour samples is known as absolute colour difference and is defined by the equation [50]:

$$\Delta H_{ab}^* = \sqrt{(\Delta a^*)^2 + (\Delta b^*)^2 - (\Delta C_{ab}^*)^2}$$

where Δa^* and Δb^* are differences in the colour coordinates a* and b* and ΔC_{ab}^* is the difference between the C* of the two samples.

The hue difference ΔH_{ab}^* is positive if the hue angle h* of the samples is greater than that of the target and negative if the ΔH^* of the samples is less than that of the target.

2.4. Statistical Analysis

Statistical analyses were performed with Statistica 13 software (Dell Inc. 2016). One-way ANOVA (the factor was onion cultivar) was performed on the thrips actual count, the proportional abundance of thrips, and the colour measurement data (L*, a*, b*, C*, and h). For statistical analysis, the data regarding the thrips actual count were normalized using $\log_{10}(x + 1)$ transformation; for the proportional abundance of thrips (%), arcsine transformation was used. The tables and figures contain untransformed data. The Shapiro–Wilk test was used to check the distribution of the data, and Levene’s test was used to check homogeneity of variance. Multiple comparisons were computed by using Duncan’s multiple range test ($p < 0.05$). To examine the relationship between the actual count and proportional abundance of thrips and leaf colour parameters; Pearson’s correlation coefficient (r) was calculated, and significance was set at $p < 0.05$.

3. Results

3.1. Evaluation of Thrips Abundance

In 2015, significant variability of cultivars was found in terms of the actual count ($F = 5.958$; $df = 7$; $p < 0.000$) and proportional abundance of adult thrips ($F = 5.320$; $df = 7$; $p < 0.001$) collected directly from onion plants. In addition, the actual count and proportional abundance of thrips collected from onion plants with a sweeping net were significantly affected by the cultivar ($F = 10.67$; $df = 7$; $p < 0.000$ and $F = 11.029$; $df = 7$; $p < 0.000$, respectively). There was only no block effect on the proportional abundance of adult thrips collected directly from plants ($p = 0.058$).

A significantly higher mean number of onion thrips was collected directly from Niagara F₁ and Bila plants in comparison with the other cultivars except for Karmen, Kristine, and Polanowska. Alibaba and Tęcza fell into the second homogenous group when Duncan's test was performed, while Wenta was infested with the lowest number of thrips (Figure 3a). The proportional abundance of thrips showed the biggest differences between cultivars in terms of susceptibility to *T. tabaci* infestation; Niagara F₁ and Bila attracted the most adult thrips, while Wenta was the least infested (Figure 3b).

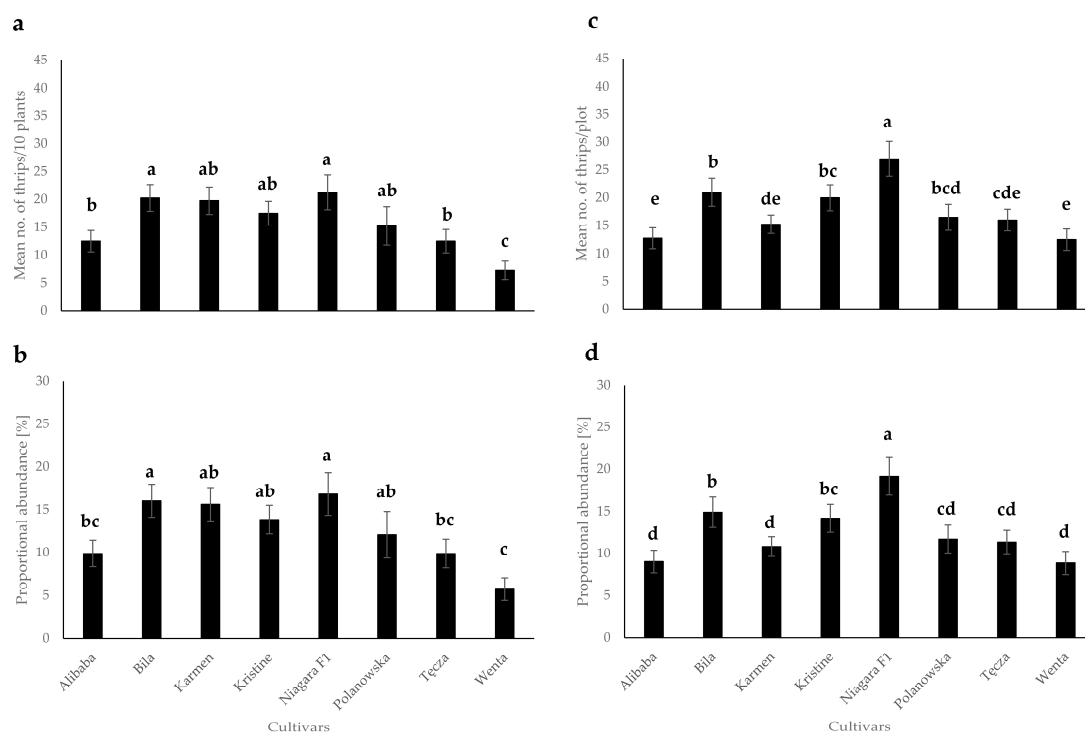


Figure 3. Actual count (mean \pm SE) and proportional abundance of *Thrips tabaci* adults collected (a,b) directly from plants and (c,d) with sweep net during onion plant colonization by thrips in 2015. Means with the same letters on each bar are not significantly different (Duncan's Multiple Range Test $p < 0.05$).

An almost identical order of susceptibility to thrips infestation was established by the actual count of thrips collected with a sweep net and directly from plants. Sweep net sampling caught more *T. tabaci* adults on all cultivars. A significant difference was found between the most infested cultivar, Niagara F₁, and all the other tested cultivars. Alibaba and Wenta were infested with the lowest number of thrips (Figure 3c). Niagara F₁, a cultivar susceptible to thrips infestation, had significantly the highest proportional abundance of onion thrips compared with the other onion genotypes. In contrast, the least infested cultivars Alibaba, Wenta, and Karmen had significantly the lowest proportional abundance of thrips (Figure 3d).

Significant variability of cultivars was also found in 2016 in terms of actual count and proportional abundance of adult thrips collected directly from onion plants ($F = 22.916$; $df = 7$; $p < 0.000$ and $F = 17.655$; $df = 7$; $p < 0.000$, respectively) and collected with a sweep net ($F = 10.983$; $df = 7$; $p < 0.000$ and $F = 11.58$; $df = 7$; $p < 0.000$, respectively). There was no block effect on the actual count or proportional abundance of adult thrips collected with a sweep net ($p = 0.533$ and $p = 0.470$, respectively).

In 2016, for the mean number and proportional abundance of thrips collected directly from plants, Duncan's test produced three homogenous groups from the eight onion cultivars. Six were thrips-susceptible: Alibaba, Karmen, Kristine, Niagara F₁; and Polanowska and Wenta, and in the second group one genotype, Bila, and in the third group one genotype, Tęcza, were the least susceptible to onion thrips infestation (Figure 4a,b).

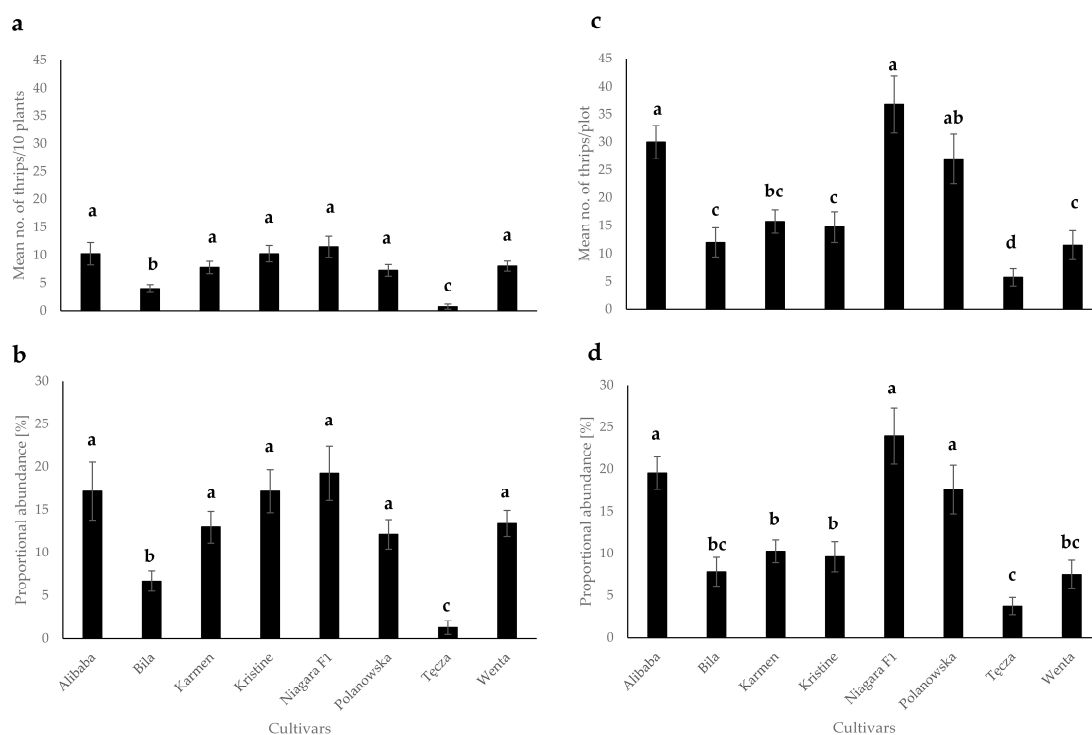


Figure 4. Actual count (mean \pm SE) and proportional abundance of *Thrips tabaci* adults collected (a,b) directly from plants and (c,d) with sweep net during onion plant colonization by thrips in 2016. Means with the same letters on each bar are not significantly different (Duncan's Multiple Range Test $p < 0.05$).

The mean number of onion thrips specimens collected with a sweep net from Niagara F₁ and Alibaba differed significantly from that collected from the other tested cultivars, except for only Polanowska. Tęcza was infested with the lowest number of thrips, followed by Wenta, Bila, and Kristine (Figure 4c). Susceptible onion cultivars had again a significantly higher proportion of thrips adults than less infested ones. Niagara F₁, Polanowska, and Alibaba attracted the most thrips; Tęcza was the least attractive for infestation, followed by Wenta and Bila (Figure 4d).

3.2. Measurement of Onion Leaf Colour

In 2015, there was a significant effect of variety ($p < 0.05$) on all computed colour variables and only the a* blocks in the L*a*b* colour space analysis were not significant (Table 1). The coordinate L*, which determines the lightness of the onion leaves, was the highest for the thrips infestation-susceptible Bila (Table 1, Figure 1). In contrast, the lowest lightness was determined for the least attractive cultivar Wenta. In addition, low lightness was recorded for Kristine, Polanowska, and Tęcza, and the mean L* value of these cultivars fell into the same homogenous group as Wenta when Duncan's test was performed

(Table 1). All the coordinate a^* values were negative, indicating dominance of green rather than red colour. Bila had the significantly lowest a^* value in comparison with all other cultivars, which indicates the most intensive green colour. In turn, all the b^* values were positive, indicating the dominance of yellow colour over blue. For coordinate b^* as well as for colour saturation (C^*), Duncan's test produced three homogenous groups. Bila had the highest mean values of b^* and C^* . The moderately susceptible cultivar Tęcza was in the second homogenous group, while the six other varieties formed the third group, with the lowest b^* value found for Wenta. For hue angle, h^* , the Duncan test produced two homogenous groups, and the varieties Bila and Tęcza differed significantly from Alibaba and Polanowska (Table 1).

Table 1. Colorimetric characteristics of onion leaves in 2015.

Cultivar	L*a*b* Colour Space			L*C*h Colour Space	
	L* ¹	a*	b*	C*	h*
	Mean [±SE]				
Alibaba	45.98 ± 1.04 bc ²	−6.89 ± 0.18 b	9.88 ± 0.88 c	12.07 ± 0.82 c	−54.75 ± 1.76 c
Bila	48.64 ± 0.45 a	−7.44 ± 0.24 a	15.08 ± 1.04 a	16.82 ± 1.03 a	−63.58 ± 0.84 a
Karmen	46.61 ± 0.39 bc	−6.41 ± 0.19 b	10.16 ± 0.68 c	12.02 ± 0.68 c	−57.56 ± 1.09 bc
Kristine	44.89 ± 0.58 c	−6.88 ± 0.22 b	10.64 ± 0.52 c	12.68 ± 0.54 c	−57.03 ± 0.84 bc
Niagara F1	47.68 ± 0.73 ab	−6.57 ± 0.13 b	10.54 ± 0.12 c	12.42 ± 0.16 c	−58.07 ± 0.30 b
Polanowska	45.29 ± 0.98 c	−6.39 ± 0.08 b	9.20 ± 0.71 c	11.22 ± 0.62 c	−54.89 ± 1.08 c
Tęcza	45.80 ± 0.36 c	−6.83 ± 0.08 b	13.36 ± 0.67 b	15.01 ± 0.64 b	−62.78 ± 0.90 a
Wenta	44.79 ± 0.36 c	−6.61 ± 0.16 b	9.54 ± 0.56 c	11.62 ± 0.55 c	−55.12 ± 2.14 bc
F cultivar	5.740	4.520	13.384	12.183	13.170
p cultivar	0.000	0.003	0.000	0.000	0.000
F blocks	4.010	2.380	5.344	4.961	5.230
p blocks	0.02	0.098	0.006	0.009	0.007

Note: ¹L* in L*a*b* colour space is the same as the L* of the L*C*h colour space; ²means within a column followed by the same letter(s) are not significantly different (Duncan's Multiple Range Test $p < 0.05$).

In 2016, significant variability of cultivars was found in terms of all computed colour characteristics ($p < 0.05$). There was a nonsignificant block effect on all colour coordinates (Table 2). The highest lightness of the onion leaves was determined for two thrips infestation-susceptible cultivars, Alibaba and Kristine, in comparison with all other cultivars (Figure 2, Table 2). The mean a^* and b^* values for leaves of any cultivar were greater in 2016 than in 2015. Two of the cultivars most inhabited by onion thrips, Alibaba and Kristine, had the lowest value of a^* and the highest of b^* . Both cultivars were also characterized by the highest colour saturation (C^*), and cultivar Alibaba had the widest hue angle (h^*) (Table 2). In contrast, the least infested cultivar, Tęcza, had the highest value of a^* and the lowest value of b^* and C^* , and the narrowest hue angle (Figure 2, Table 2).

Table 2. Colorimetric characteristics of onion leaves in 2016.

Cultivar	L*a*b* Colour Space			L*C*h Colour Space	
	L* ¹	a*	b*	C*	h*
	Mean [±SE]				
Alibaba	50.24 ± 0.72 a ²	−9.87 ± 0.13 a	22.27 ± 0.63 a	24.36 ± 0.63 a	−66.05 ± 0.38 a
Bila	46.05 ± 0.23 b	−8.98 ± 0.07 b	17.75 ± 0.47 b	19.92 ± 0.45 b	−63.14 ± 0.46 b
Karmen	46.04 ± 0.41 b	−8.88 ± 0.22 b	17.69 ± 0.76 b	19.79 ± 0.77 b	−63.28 ± 0.55 b
Kristine	49.10 ± 0.80 a	−9.78 ± 0.21 a	20.51 ± 1.18 a	22.73 ± 1.16 a	−64.37 ± 0.78 ab
Niagara F1	47.18 ± 0.66 b	−8.73 ± 0.25 b	17.90 ± 1.22 b	19.93 ± 0.55 b	−63.95 ± 1.02 ab
Polanowska	46.11 ± 0.28 b	−9.05 ± 0.07 b	17.45 ± 0.39 b	19.66 ± 0.36 b	−62.56 ± 0.48 b
Tęcza	46.15 ± 0.66 b	−8.76 ± 0.20 b	16.83 ± 2.23 b	18.98 ± 1.08 b	−62.34 ± 0.97 b

Wenta	46.82 ± 0.35	-8.92 ± 0.15 b	17.90 ± 0.75 b	20.01 ± 0.75 b	-63.44 ± 0.50 b
F cultivar	8.040	6.270	4.961	5.230	2.660
p cultivar	0.000	0.000	0.001	0.001	0.039
F blocks	0.760	1.440	0.193	0.266	0.260
p blocks	0.526	0.259	0.900	0.849	0.851

Note: ¹L* in L*a*b* colour space is the same as the L* of the L*C*h colour space; ²means within a column followed by the same letter(s) are not significantly different (Duncan's Multiple Range Test $p < 0.05$).

In 2015, the highest hue difference (absolute colour difference ΔH^*) was established between Bila and Alibaba, and Polanowska and Wenta ($\Delta H^* > 2.0$), while in 2016 between Alibaba and Bila, Karmen, Tęcza and Wenta ($\Delta H^* \geq 1.0$), respectively (Tables 3 and 4).

Table 3. Absolute colour difference (ΔH^*) between leaf colours of onion cultivars in 2015.

Cultivar	Alibaba	Bila	Karmen	Kristine	Niagara F ₁	Polanowska	Tęcza	Wenta
Alibaba	x	2.15	0.57	0.46	0.66	-0.13	1.85	0.05
Bila	-2.15	x	-1.48	-1.67	-0.83	-2.04	-0.22	-2.06
Karmen	-0.57	1.48	x	-0.13	0.09	-0.53	1.21	-0.51
Kristine	-0.46	1.67	0.13	x	0.30	-0.42	1.39	-0.41
Niagara F ₁	-0.66	1.40	-0.09	0.19	x	-0.62	1.14	-0.60
Polanowska	-0.03	2.04	0.53	0.42	0.62	x	1.76	0.03
Tęcza	-1.85	0.22	-1.21	-1.39	-1.14	-1.76	x	-1.76
Wenta	-0.05	2.06	0.51	0.41	0.60	-0.03	1.76	x

Table 4. Absolute colour difference (ΔH^*) between leaf colours of onion cultivars in 2016.

Cultivar	Alibaba	Bila	Karmen	Kristine	Niagara F ₁	Polanowska	Tęcza	Wenta
Alibaba	x	-1.11	-1.06	-0.67	-0.80	-1.34	-1.37	-1.00
Bila	1.11	x	0.05	0.47	0.28	-0.38	-0.25	0.11
Karmen	1.06	-0.05	x	0.42	0.22	-0.25	-0.30	0.06
Kristine	0.67	-0.47	-0.42	x	-0.18	-0.69	-0.73	-0.36
Niagara F ₁	0.80	-0.28	-0.22	0.18	x	-0.49	-0.55	-0.18
Polanowska	0.77	0.20	0.25	0.69	0.49	x	-0.06	0.31
Tęcza	1.37	0.25	0.30	0.73	0.55	0.06	x	0.37
Wenta	1.00	-0.11	-0.06	0.36	0.18	-0.31	-0.37	x

3.3. Correlations between Thrips Occurrence and Colour Parameters

In both years, positive significant correlation was detected between lightness (L*), coordinate b*, colour saturation (C*), and hue angle (h*), and the actual count and proportional abundance of thrips collected directly from plants. In addition, a positive significant correlation was detected between L*, a*, C*, and h*, and the actual count and proportional abundance of thrips collected with a sweep net in 2015 (Tables 5 and 6). In contrast, there was a significant negative correlation between coordinate a* and the actual count and proportional abundance of thrips collected directly from plants in 2015, and between a* and the proportional abundance of thrips collected directly from plants in 2016 (Tables 5 and 6).

Table 5. Pearson's correlation between colorimetric characteristics of onion leaves and actual count and proportional abundance of adults *Thrips tabaci* in 2015 (n = 32).

Colour Coordinates	Thrips Adults Collected Directly from Plants				Thrips Adults Collected with Sweeping Net			
	Actual Count		Proportional Abundance		Actual Count		Proportional Abundance	
	r	p	r	p	r	p	r	p
L*	0.739	0.000	0.759	0.000	0.644	0.000	0.625	0.000
a*	-0.441	0.011	-0.454	0.009	-0.365	0.040	-0.343 ns	0.055
b*	0.471	0.006	0.464	0.007	0.0466	0.007	0.428	0.014
C*	0.472	0.006	0.467	0.007	0.460	0.008	0.423	0.016
h*	0.448	0.010	0.448	0.010	0.441	0.011	0.441	0.011

Note: bold r coefficient values designate significant correlation at $p < 0.05$; ns— not significant at $p < 0.05$.

Table 6. Pearson's correlation between colorimetric characteristics of onion leaves and actual count and proportional abundance of adults *Thrips tabaci* in 2016 (n = 32).

Colour Coordinates	Thrips Adults Collected Directly from Plants				Thrips Adults Collected with Sweeping Net			
	Actual Count		Proportional Abundance		Actual Count		Proportional Abundance	
	r	p	r	p	r	p	r	p
L*	0.390	0.027	0.526	0.002	0.255 ns	0.158	0.198 ns	0.275
a*	-0.333 ns	0.062	-0.417	0.017	-0.174 ns	0.341	-0.732 ns	0.691
b*	0.371	0.036	0.463	0.008	0.316 ns	0.078	0.255 ns	0.157
C*	0.372	0.036	0.464	0.007	0.305 ns	0.089	0.239 ns	0.186
h*	0.410	0.020	0.410	0.020	0.365	0.039	0.365	0.039

Note: bold r coefficient values designate significant correlation at $p < 0.05$; ns— not significant at $p < 0.05$.

4. Discussion

The measurement of onion thrips population size under field conditions is used by entomologists as a tool for the first stage of selecting resistant plant material. Antixenosis testing is essentially based on measuring the attractiveness of a plant genotype to colonizing adult thrips. Fail et al. [51] proposed using the proportional abundance of thrips adults in addition to the actual count of thrips as an appropriate measure of antixenosis because it seems to be more stable under varying field conditions. Proportional abundance is also more in line with the concept that resistance of plants is relative and is based on comparison with plants lacking the resistance characters, i.e., susceptible plants [52]. According to Fail et al. [51], the heat sum model predicts the development of *T. tabaci* well, and therefore all thrips adults that we encountered during the sampling events in both years can be considered as colonizing adults. The term antixenosis cannot be used at a later time when newly emerged individuals appear on onions.

In two consecutive years, 2015 and 2016, a different order of the level of susceptibility of onion cultivars to *T. tabaci* was established. In 2015, the cultivar Wenta followed by Alibaba showed a low level of susceptibility to colonization by onion thrips, which was reflected in both low actual count and proportional abundance of thrips collected directly from plants and with a sweep net. In 2016, the cultivars Tęcza and Bila were the least susceptible. The proportional abundance of onion thrips collected directly from Tęcza in 2015 and collected from Wenta with a sweep net in 2016 also indicated a low level of attractiveness of these cultivars to onion thrips. In contrast, the cultivars most susceptible to onion thrips infestation were Niagara F₁ and Bila in 2015, and Alibaba and Kristine in 2016.

The observed preference among leaves of different cultivars could have been the result of thrips choosing landing sites among the leaves of the available plants. The decision on the suitability of a plant as a host is made in the very first phase of host selection, with

colonizers using both visual and chemical cues [15]. Thrips might show a preference for a specific odour, hue, or intensity of colour in their preferred plant [10,53]. The selection process can be disrupted under field conditions. Thrips are relatively weak flyers, being able to determine their speed and direction only at low wind speeds [54,55]. As a consequence, only a very small proportion of thrips locate suitable hosts [54]. The other reason for the lower abundance of thrips on some cultivars compared to those more colonized could be the result of more rapid take-off after landing on the leaves of a resistant variety [51]. In our study, the low number of onion thrips on Tęcza and Wenta in two consecutive seasons may indicate host plant selection and nonpreference mechanism of resistance (antixenosis). Nonetheless, to confirm this mechanism of resistance to plant colonization by *T. tabaci*, a choice test should be performed under controlled conditions.

We found distinct differences in some computed colour variables between the leaves of the onion cultivars most and least susceptible to *T. tabaci* infestation, but because of the discrepancy in the results between the two years of the study, the role of visual cues for thrips must be interpreted with caution. By analysing the results for the eight onion cultivars, we have ascertained that leaf colour may influence colonization by thrips. In both years, the cultivars with the highest value for lightness (Bila and Niagara F₁ in 2015, and Alibaba and Niagara F₁ in 2016) were very attractive to *T. tabaci*. In contrast, the resistant cultivars, Wenta in 2015 and Tęcza in 2016, were darker and had low L* values. A negative coordinate a* value indicates a green colour; for susceptible cultivars, namely Bila in 2015, and Alibaba and Kristine in 2016, its value decreased, so the tonality of the colour shifted to greener. In turn, the increasing positive value of coordinate b* (yellowness) indicated that the leaf colour of susceptible cultivars was oriented towards yellow. In contrast, the increasing value of a* in resistant cultivars, Wenta in 2015 and Tęcza in 2016, and lower value of b* indicated a less intense green colour oriented towards yellow-grey. The lower value of C* in these resistant cultivars means that their colour is less saturated in comparison with susceptible ones with a high chroma. Estimation of the hue difference (ΔH^*_{ab}) and hue angle h* indicated that the colour of the cultivars most colonized by onion thrips had a more yellowish hue while that of the least infested plants was more grey. Colorimetric values of leaf colour were correlated with attractiveness to thrips: typically, higher b*, C*, and h* values and lower a* attracted more thrips; therefore, we concluded that the vivid, intense green-yellowish leaf colour of susceptible varieties might have been the cause of the observed thrips preference. The peak sensitivity of *T. tabaci* photoreceptors at 540–570 nm [27] could perhaps partially explain the preference for the light green-yellowish colour. In contrast to our results, Diaz-Montano et al. [10] found that onion varieties resistant to *T. tabaci* such Tioga, OLYSO5N5, and Peso had visually determined yellow-green leaves unlike the bluish-green foliage of susceptible cultivars SYN-G2 and Santana. These observations were usually accompanied by high b* values measured in the resistant cultivars in comparison with the susceptible ones, but some resistant varieties had a b* value very similar to that of the susceptible ones. Fail et al. [39] found significant differences in the CIE 1976 a* and b* values between leaves forming the head of resistant and susceptible varieties of cabbage. The moderately resistant variety Blokotor had the highest negative value of coordinate a* and the lowest value of coordinate b* in comparison with two other resistant (yellowish-green) as well as three susceptible cultivars (yellowish). In other studies, Alimousavi et al. [56], Biriithia et al. [57], and Yousefi et al. [58] showed that onion genotypes with glossy foliage and a light green colour had lower thrips infestation in comparison with nonglossy and medium or dark green susceptible genotypes. Poboźniak [59] found that pea cultivars with grassy green leaves were the most frequently infested by *T. tabaci*. At the same time, cultivars with yellow-green leaves or dark blue-green leaves were less attractive to thrips.

Behavioural variability between studies may reflect the geographical distribution and genetic differences of onion thrips [31,32]. It may also relate to differences in experimental designs. In contrast to our research, the authors of the above-mentioned studies

included thrips collected throughout the entire growing season, i.e., also individuals already reproducing on onion leaves; their presence on plants cannot be considered as the result of thrips choice and could be affected by antibiosis.

Our results are concordant with those of the study carried out by Westmore et al. [29], who reported that potato cultivars preferred by adult onion thrips during colonization for foraging usually had lighter green foliage and higher spectral reflectance in the green wavelength (552 nm). In contrast, more eggs were laid on potato leaves with darker green foliage [29]. Understanding the factors underlying the choice of both host and oviposition is important for guiding breeding programmes for new cultivars.

The environmental conditions that a plant is exposed to, including soil properties, weather, and its phenological age, alter the optical properties of its leaves [60]. It is highly probable that environmental stress might have affected the leaf colour of onion cultivars, and therefore colorimetric values of some onion cultivars were different in the two years. Therefore, the manager of the onion-breeding programme should plant the same check varieties each year to determine how the colour parameters may have shifted. In our experiment, the very high attractiveness of Bila for thrips infestation in 2015 might have been related to the higher lightness and higher values of b^* , C^* , and h^* and lower value of a^* for Bila compared to 2016.

Although it is difficult to ascertain which colour characteristic contributed most to the differences in susceptibility of onion leaves to onion thrips; we suspect that lightness may be one of the key factors associated with varietal attractiveness. In both years, the cultivar most attractive for thrips infestation, Niagara F₁, had a very high lightness value, while the a^* and b^* values were similar to those of the moderately resistant varieties. In addition, the high correlation ($r > 0.6$) between the actual count and proportional abundance of *T. tabaci*, and the lightness values measured for the onion leaves in 2015 might indicate a high preference of *T. tabaci* for cultivars with lighter leaves.

Reflectance values within a spectral range have been correlated with thrips attraction, usually with higher reflectance attracting higher numbers of thrips. Diaz-Montano et al. [38] found that *T. tabaci* abundance and the brightness of onion leaves were significantly correlated, especially in the UV range of light (275–375 nm and 310–410 nm). The same authors created the hypothesis that *T. tabaci* prefer onion cultivars that reflect a greater amount of light; it is possible that this characteristic may shelter onion thrips from heat and may make these onion cultivars a more preferable host. In addition, Fail et al. [51] found a positive correlation between the actual count of thrips adults and the brightness of old cabbage leaves. Besides the average brightness (between 270 and 650 nm), the reflectance in the range of sensitivity of the first (275–375 nm), second (275–400 nm), and third (400–650 nm) theoretical photoreceptor systems of *T. tabaci* adopted by the authors was almost equally correlated with thrips abundance.

Brightness is related to reflectance, while lightness (L^*) is more related to the colour impression. A colour surface with a higher L^* value usually has a higher reflectance [61]. Reflectance is a physical measure that depends on the incidence angle, the polarization of the radiation, and the refraction index of the surface [62]. The reflection of light from the leaf and transmission through the leaf are determined by the wavelengths of light absorbed by the various biochemical compounds in leaves (chlorophylls, carotenoids, water, cellulose and lignin, proteins, etc.) and also depend on the epidermis, waxes, cutin, and protrusions such as leaf hairs [63,64]. Thus, for leaves with the greatest concentrations of chlorophylls, carotenoids, water, cellulose and lignin, proteins, etc., reflectance is the smallest at a certain wavelength. Lighter leaves usually reflect much of the visible light [64]. In our results, cultivars with lighter, green-yellowish leaves attracted thrips the most, which could be due to their higher reflectance; however, more evidence supporting this and additional work are needed to understand the relationship between the optical properties of leaves and the responses of onion thrips to different colour attributes.

It should be noted that colour is only one component that contributes to the appearance of onion plants. Shape, leaf angle, plant height, and insect or disease damage also

contribute to the appearance of a plant [56,65,66]. In turn, the micromorphology of the leaf epidermis, internal leaf structure, and chemical properties might affect thrips post lighting behaviour [67,68].

5. Conclusions

Despite the complication of interaction, we ascertained that plant colour significantly influences the level of varietal infestation by onion thrips. We identified useful genotypes, Tęcza and Wenta, for host plant resistance in onions to *T. tabaci*, and suggest a link between colour and antixenotic resistance, so that breeding for host plant resistance can be advanced more quickly. Direct evidence of preference by *T. tabaci* for a vivid, intense green-yellowish colour on onion was determined while the resistant cultivars had darker, green-grey-yellowish leaves. Additionally, the genetic basis of colour in onions and its influence on the behaviour of *T. tabaci* warrant further investigation. We acknowledge that additional factors, including foliar volatiles, are likely to further influence host choice. At the same time, it should also be realized that antixenosis may not be the only resistance mechanism at work in onion thrips' resistance in onion.

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10.3. Publikacja nr 3

Article

Anatomical and Biochemical Traits Associated with Field Resistance of Onion Cultivars to Onion Thrips and the Effect of Mechanical Injury on the Level of Biochemical Compounds in Onion Leaves

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Abstract: *Thrips tabaci* Lind. is a global pest and also represents a serious threat to onion production in Poland. In 2 years (2015–2016) of field studies, 8 onion cultivars were evaluated to characterize the resistance to onion thrips and to determine if any biochemical and anatomical features of onion plants are associated with antixenotic and/or antibiotic mechanisms of resistance. Additionally, the influence of mechanical injury on the content of several biochemical compounds in onion leaves was made. The resistance to thrips colonization during the migration period, abundance, and thrips damage throughout the whole vegetation season was determined. We identified two cultivars, Tęcza and Wenta, resistant to thrips colonization and abundance, and one cultivar Wenta resistant to thrips damage. A positive correlation between concentrations of the reducing sugars and thrips abundance and conversely negative relationships between the total phenolic content and thrips damage was confirmed in both years. We suspect that a thinner epidermal layer, a smaller area of epidermal and mesophilic cells, and a lower diameter of vascular bundles may favor the resistance of onion cultivars to thrips. Thrips foraging resulted in a decrease in the content of soluble sugars, sucrose, and plant pigments in the leaves of all onion varieties.

Keywords: antixenosis; antibiosis; sugars; phenolics; chlorophyll; carotenoids; epidermis; mesophyll; vascular bundles

1. Introduction

Onion is an important vegetable in terms of global production volume. The largest onion-producing countries are China and India, whose combined share of global production is approaching 46.5% [1]. Among EU member states, most onions are harvested in the Netherlands, Spain, and Poland with 651,349 tons yearly production, putting Poland in 3rd position and constituting approximately 8.3% of the harvest in the European Union [2].

Onion thrips, *Thrips tabaci* Lind. is a global pest [3,4] and also represents a serious threat to onion production in Poland [5]. Adults and larvae of onion thrips insert their stylets into the leaves and ingest the content of epidermal and mesophyll cells [6]. The pierced cells collapse or fill up with air, giving the damaged area a silvery appearance [7]. Therefore, damage resulting from injuries caused by thrips appears as silvery patches,

streaks on the leaves, or tiny black “tar” spots, which are thrips feces. As a result, the feeding thrips cause premature senescence of leaves, reduce the photosynthetic capacity, hinder the transport of nutrients to the bulb, and consequently lead to their distortion and loss of biomass [3,8]. Thrips damage can significantly reduce onion yields ranging from 22% [9], 30% [10], 35–43% [11], to up to 60% [12]. Onion thrips are a vector of Iris yellow spot virus (IYSV) and they spread it efficiently in onion plantations [13]. Moreover, tissue injury that results from thrips feeding causes increased vulnerability to infection by bacterial pathogens such as *Pantoea ananatis*, *P. agglomerans*, and *P. alli* that cause the onion center-rot complex, as well as *Alternaria porri*, the fungus that in turn causes purple blotch [14,15]. Thus, to prevent the opening of infection pathways, it is usually necessary to combat onion thrips, which requires frequent applications of insecticides [16], with the unfortunate consequence of increased resistance to commonly used pyrethroids and organophosphates [17,18], methomyl, and oxamyl (carbamates), abamectin [19], and spinetoram [20].

Consumer demand for high-quality onions, free from pesticide residues are currently increasing. For this reason, a growing number of onion growers are choosing the cultivation of resistant and/or tolerant cultivars as an important preventative element of Integrated Plant Management (IPM) [21].

Resistant cultivars have physical and/or chemical traits that protect them against pest infestation and feeding [22]. The cultivation of cultivars with even partial resistance is considered to be the best method of pest control [23]. Resistance mechanisms can be classified as antixenosis and antibiosis. These insect plant host relationships relate to two different events, namely the search by an insect for the plant and its unacceptance (antixenosis), and the impact of the plant as food on the pest (antibiosis) [24,25]. Plant antixenosis negatively affects insect colonization processes, resulting in a reduced initial infestation level, due to a feature (or set of features) that deters insects from settling and feeding [24]. The expression of antixenosis in genotypes may be a consequence of morphological, physical, and chemical features in plants and mainly affects the visual [26,27] and olfactory stimuli [28] involved in the host-finding behavior of thrips. In contrast, antibiosis negatively affects insect pest biology and their progeny (survival, development, and reproduction) and are strongly influenced by the poor plant's nutritional quality (inadequate composition and concentration of soluble proteins and carbohydrates) [29,30], primary metabolites (e.g., lectins, proteinase, and amylase inhibitors), and secondary plant compounds (e.g., chlorogenic acid, glycoalkaloids, flavonoids, jasmonic acid) [31,32].

In the multi-cultivar planted trial, i.e., in a choice situation, some of the differences in thrips population development can be attributed to differences in thrips preference and/or host plant resistance. Under environmental conditions, the measurement of insect population size in the field is used by entomologists as an opportunity to conduct the first stage of selection of susceptible or resistant plant material. The existence of plant resistance can indicate that the plant possesses a mechanism of antixenosis and/or antibiosis. The development and survival of thrips on crops in the field not only depend on the resistance of host plants but are also highly influenced by environmental conditions, including temperature, wind, frequency and the level of precipitation during the vegetation phase [33], as well as predators [34] and parasitoids [35].

Currently, there are no known onion cultivars that are very highly resistant to onion thrips, but some of them show a certain level of resistance, mainly related to the morphological, physical, and chemical characteristics of onion plants. In studies conducted in New York (USA), 15 cultivars considered as partially resistant to thrips were identified (out of 54 tested onion cultivars), namely, OLYS05N5, Tioga, Peso, Gramero, Cometa, Medeo, T-433, Colorado 6, Mesquite, Acero, White Wing, Calibra, Delgado, NMSU 03-52-1, and Vaquero [13,26]. Results obtained by Diaz-Montano et al. [13,26] indicated that all of these onion varieties had yellow-green leaves and showed a strong antixenotic effect; furthermore, the last six cultivars showed an intermediately high antibiotic effect on onion thrips. Moreover, subsequent research showed that onion varieties with lighter-green and glossy leaves usually supported a lower number of onion thrips and suffered less feeding damage than phenotypes with waxy,

bluish-green leaves [8,36]. According to Damon et al. [36], the light-green leaf colour in resistant onion varieties has been associated with the amount and chemical composition of epicuticular waxes on foliage. Varieties resistant to onion thrips with glossy (low wax) and semi-glossy (intermediate wax) phenotypes had much lower amounts of the ketone hentriacontanone-16(H-16) and higher amounts of other waxes such as alkanes and fatty alcohols compared to varieties with phenotypes susceptible to thrips feeding [37]. In Brazil, the antixenotic resistance of the variety Alfa São Francisco RT was associated with certain morphological traits, a wider central angle (16.4°), a thinner cuticle, a larger amount of epicuticular waxes, and stomata on the surface of leaves, while the antibiotic resistance of BR 29 and Sirius was likely due to the presence of resistance-conferring substances or high amounts of some component in the chemical composition of plants [38]. Alimousavi et al. [39] also confirmed that in the four Iranian onion cultivars Meshkan, Sefid-e-Kurdistan, Sefid-e-Qom, and Eghlid, a large angle between the two innermost emerged leaves, especially in the young plant, help to restrict the thrips population by reducing the protective environment to a minimum. In Tanzania, out of 163 onion accessions, only three onion thrips resistant accessions (VI038512, VI038552, and AVON 1067) were identified [40]. The explanation of biophysical and biochemical bases of resistance revealed that a wider leaf angle, higher leaf toughness, and higher amount of total phenolics influenced the defensive reaction of these onion accessions to thrips feeding. Varietal preference and the susceptibility of onion plants to onion thrips have been documented in Poland, but only some traits were investigated to explain this preference [41,42].

An in-depth understanding of the features underlying the resistance of onion cultivars to thrips is essential for breeders to improve the resistance of onion cultivars to this pest. Therefore, this research was conducted with the following aims: (1) to identify onion cultivars possibly resistant to onion thrips infestation in the early growing season, resistant to thrips abundance and damage under field conditions throughout the whole growing season; and (2) to determine whether there is a relationship between any biochemical and anatomical features of onion plants and their resistance to thrips. Additionally, an attempt was made to determine the influence of mechanical damage on the content of several biochemical compounds in the leaves of the onion cultivars examined.

2. Materials and Methods

2.1. Plant Material and Experimental Setup

All of the *Allium cepa* L. cultivars applied in this study 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 (mid-early cultivar Alibaba with a white bulb, late cv. Bila, mid-late cultivars Kristine, and Niagara F₁ with a yellow bulb and late cv. Wenta with a red bulb), Polan in Krakow (mid-early cv. Karmen with a red bulb and mid-late Polanowska with a yellow bulb) and Spójnia in Nochowo (early cv. Tęcza with a yellow bulb). Preliminary screening, of a large number of new and F₁ hybrid cultivars, conducted beforehand indicated that the eight selected cultivars might possess some traits responsible for resistance or tolerance to the onion thrips [41].

Trials were conducted at the Experimental Station of the University of Agriculture in Krakow which is located in Mydlniki (southern Poland, Krakow District, 50°04' N, 19°51' E, 207 m above sea level). The cultivation was carried out on a typical brown soil with a pH of 6.5 with 18 g/kg organic carbon content; all agronomic treatments were carried out following the recommendations for this crop type. In the spring of each trial year, plots were fertilized according to the Integrated Production recommendations for onion in the field. No chemical treatments were applied; weeds were removed mechanically and manually.

The experimental design was arranged in a randomized complete blocks (RCB) design with four blocks. The plot size was 12 m² (3 × 4 m), with a distance between the plots of 1 m. Seeds were sown (25 kg/ha) in rows, 0.3 m apart, on 10 April 2015 and 6 April 2016. The onion plots were separated from the neighboring crops (potatoes, herbs, red beets, white cabbage, zucchini, and pumpkin) by a 2 m path.

On-site meteorological data (ambient air temperature and precipitation) were recorded at the trial site from May to September in 2015 and 2016, at 60-min intervals. A HOBO water temperature Pro data logger (Onset Computer Corp., Bourne, MA, USA) was used for this purpose (Figure S1).

2.2. Field Resistance Experiment

The identification of resistance to host plant colonization (selection of plants for settlement) and determination of the abundance of the onion thrips throughout the whole season (resistance to thrips abundance) was carried out under field conditions. For this purpose, from June until harvest (end of August) within each testing plot, 10 randomly selected plants per cultivar within every block were taken weekly from the plots and placed into separate zip-lock plastic bags followed by appropriate labeling. The collected material was transported to the laboratory, where larvae and adults of thrips were hand-separated from onion plants using a soft brush (size 1) and placed in vials containing 75% ethanol. Microscopic slides were prepared under laboratory conditions according to the technique described by Zawirska [43]. The taxonomic identification was made based on keys developed by zur Strassen [44] (adults) and Kucharczyk [45] (larvae).

The identification of resistance to thrips damage was determined as the degree of damaged leaf area of onion leaves. For this purpose, every week three leaves (the oldest, the middle-aged, and the youngest) were chosen from each of 10 randomly selected plants harvested from each testing plot. Next, a 10 cm long segment was cut from the center of each leaf. Then, the onion leaf was sliced open, and the damaged leaf area (silvery spots and white blotches along with the leaves) was estimated and expressed as the percentage of the damaged leaf. In the assessment of the level of field resistance of the assigned cultivars to plant colonization by migrating adult thrips, one indicator was used, namely, the mean number of adult thrips per 10 plants collected during the migration period, which lasted from 24 June to 2 July 2015, and from 16 to 25 June 2016. Based on published data about the effect of temperature on the development of onion thrips [46,47], a degree-day (DD) model was computed for both 2015 and 2016 [42]. The heat sum model predicted the development of onion thrips well, and therefore all adult thrips that were encountered during this sampling event (for both years) can be considered colonizing adults. The seasonal mean number of feeding thrips (adults and larvae) per 10 plants and mean feeding damage expressed as a mean percentage of the damaged leaf area were used as indicators to estimate the field resistance levels throughout the growing season of the onion cultivars tested. A four-grade scale was used to define the value of the indicators (1–4). The highest numbers of points were given to samples with the lowest values for the relevant criteria, i.e., those which demonstrated the highest level of cultivar resistance. Different scales were used for the indicators in each year (2015; 2016)—the reason for this was the significant difference in the abundance of the thrips populations observed in each year (Table 1).

Table 1. The number of points assigned to indicators of the field resistance of onion cultivars to *Thrips tabaci*.

Indicators	Year	Scale			
		4 Points	3 Points	2 Points	1 Point
Mean number of migrating adult thrips per 10 plants	2015	0.00–3.75	3.76–6.75	6.76–10.75	>10.75
	2016	0.00–1.50	1.51–3.50	3.51–5.50	>5.50
Seasonal mean number of adults and larvae of thrips per 10 plants	2015	0.00–7.50	7.51–10.00	10.01–12.00	>12.00
	2016	0.00–2.75	2.76–4.75	4.76–7.00	>7.00
Mean percentage of damaged leaf area by feeding thrips	2015	0.00–10.00	10.01–13.00	13.01–17.50	>17.50
	2016	0.00–5.00	5.01–6.50	6.51–7.25	>7.25

Determination of the level of resistance was based on the mean number of points over the two years, assigned separately for the plant colonization by migrating adult thrips, resistance to thrips abundance, and the resistance to thrips damage throughout the growing

season. Four levels of field resistance were used to classify the onion cultivars: resistant—with a high degree of field resistance (>3.00 points); moderately resistant—with a moderate degree of field resistance (3.00 – 2.50 points); susceptible—with a low degree of field resistance (2.49 – 1.5 points); and highly susceptible—with a very low degree of field resistance (<1.5 points).

The onions were harvested on 10 September in 2015 and 8 September in 2016. As each cultivar has a different yield potential, bulb yields were not compared among cultivars.

2.3. Biochemical Analyses of Leaves

For biochemical studies, 6 undamaged plants and 6 damaged onion plants by thrips were taken randomly from each cultivar within every block on 28 July 2015, and 8 August 2016. Two of the middle-aged leaves with injuries caused by thrips of each damaged plant and two healthy leaves from the undamaged plants were taken. Then, the undamaged and damaged leaves were separately cut into approximately 1 cm pieces, mixed, weighed, freeze-dried, and kept in the dark at room temperature. The lyophilisates were then ground using an electric mill and 0.5 g of the ground lyophilisate was homogenized with 90% ethanol for approximately 30 s in a porcelain mortar. The obtained solutions were filtered under pressure through a G4-type sintered glass funnel (pore size: 10 – 16 μm), poured into polypropylene tubes, and filled to the final volume of 25 mL with the solution obtained by washing the mortar several times with the extractant. The extracts were stored in the dark at 4 $^{\circ}\text{C}$. Using them, all analyses of the biochemical parameters were performed. Four repetitions of measurements of all biochemical parameters were carried out for each plot in both years for undamaged and damaged onion leaves.

2.3.1. Total Soluble Sugar Content

The total soluble sugar content was determined by the anthrone test [48]. The extracts for analysis were diluted (0.02 mL of the extract and 4.98 mL of water) and the anthrone reagent (0.2 g anthrone in conc. H_2SO_4) was added and thoroughly mixed. The samples were then incubated at 90 ± 1 $^{\circ}\text{C}$ for 15 min. After cooling down, the absorbance of a blue-green complex was measured at 620 nm (JASCO V-530 UV/Vis spectrophotometer). A 5-point standard curve was prepared using glucose solutions. The data were expressed in grams per 100 g of fresh plant weight.

2.3.2. Reducing Sugar Content

The reducing sugar content was assessed by the hexacyanoferrate assay [49]. Briefly, 0.3 mL of 0.3% $\text{K}_3(\text{Fe}(\text{CN})_6)$ and 0.3 mL of 0.53% Na_2CO_3 solutions were mixed with the extract, 400x diluted with water, and heated at 90 ± 1 $^{\circ}\text{C}$ for 15 min. After cooling, 1.5 mL of 0.5% $\text{Fe}_2(\text{SO}_4)_3$ solution containing 7.5 mL of 85% H_3PO_4 and 1 g of acacia gum per 100 mL was added. After 15-min incubation at room temperature, the absorbance of a blue product, $\text{KFe}(\text{Fe}(\text{CN})_6)_2$, was measured at 660 nm (JASCO V-530 UV/Vis spectrophotometer). A 5-point standard curve was prepared using glucose solutions. The data were expressed in grams per 100 g of fresh plant weight.

2.3.3. Sucrose Content

The sucrose concentration was estimated as the difference between the concentrations of the total soluble sugars and the reducing sugars (total sugars—reducing sugars \approx sucrose).

2.3.4. Total Phenolic Content

The sum of phenolic compounds was measured according to a Folin–Ciocalteu assay [50]. A 2.4 mL sample of the extract diluted 10-fold with water was then mixed with 0.25 mL of 25% Na_2CO_3 and 0.125 mL of the Folin–Ciocalteu reagent (diluted twice with water). The absorbance was measured at 760 nm after 15-min incubation at room temperature (JASCO V-530 UV/Vis spectrophotometer). A 5-point standard curve was prepared

using gallic acid solutions and the final results were expressed as mg of GAE (gallic acid equivalents) per 100 g of fresh plant weight.

2.3.5. Chlorophyll and Total Carotenoid Contents

For the determination of chlorophyll and total carotenoid contents, the spectrum of the extracts was measured against ethanol in the range of 450–800 nm (JASCO V-530 UV/Vis spectrophotometer). The absorbance values were recorded at 3 wavelengths: 664, 648 and 470 nm. To calculate the content of chlorophyll a, chlorophyll b, and the sum of carotenoids in the plant material, the absorbance values were used in empirical equations [51]:

$$C \text{ chlorophyll a} = 11.75 \cdot A_{664} - 2.35 \cdot A_{648} \quad (1)$$

$$C \text{ chlorophyll b} = 18.61 \cdot A_{648} - 3.96 \cdot A_{662} \quad (2)$$

$$C \text{ sum of carotenoids} = \frac{1000 \cdot A_{470} - 2.27 \cdot C_{\text{chla}} - 81.40 \cdot C_{\text{chlb}}}{227} \quad (3)$$

where: (A) measured absorbance, (C) concentration of chlorophylls or carotenoids in the extract (mg/dm³).

The final results were expressed in milligrams per 100 g of fresh plant weight.

2.4. Anatomical Studies of Leaves

For anatomical studies, five-leaf blades from each cultivar were collected on 8 August 2016. Ten fragments, about 10 mm long were excised from a half-length of each leaf blade. Tissue samples were fixed in a glutaraldehyde solution and washed thoroughly with 0.1-M phosphate buffer. After dehydration in a graded ethanol series, the samples were immersed in acetone and embedded in Epon 812 resin. The sections, 1 µm thick, were cut with a diamond knife on a Tesla 490A ultramicrotome, stained with 0.1% methylene blue, and examined in an Axio Imager M2 (Zeiss), with observations conducted in the bright field. Measurements of leaf blade anatomical parameters on the cross-sections from each leaf were conducted with the use of Image software. The leaf-blade thickness was measured separately along the vascular bundle axis (referred to as max. thickness) and only through the mesophyll layers (referred to as min. thickness). The mean leaf blade thickness was calculated as the arithmetic mean of these values. Furthermore, epidermal cell thickness, perimeter, and area were also measured. Within the mesophyll, the perimeter and area of the cells were estimated, together with the number of cell layers and intracellular spaces. Additionally, measurements of the diameter, perimeter, area, and distance between leaf vascular bundles were made.

2.5. Studies on the Effect of Mechanical Injury on the Level of Biochemical Compounds in Onion Leaves

For this study, the total soluble sugar, reducing sugar, sucrose, total phenolic, chlorophyll a and b, and the total carotenoid contents in the leaves of onion plants both undamaged and damaged by feeding thrips were compared, in both years.

2.6. Statistical Analysis

Statistical analyses were performed with the Statistica 13 software (Dell Inc., United States, 2016). For all one-way ANOVA analyses (the factor was onion cultivar), residual plots were checked for normality of residuals. In the case of the absence of normality, the data regarding the number of thrips were normalized using log₁₀(x + 1) transformation; for the damaged leaf area (%), arcsine transformation and ln transformation for the leaf blade thickness and parameters of the leaf's epidermal and mesophyll cells were used. Note that the tables and figures show untransformed data. Multiple comparisons were computed using Duncan's multiple range test (*p* < 0.05). Two-way ANOVA was performed with cultivars and damage level of leaves (undamaged/damaged leaves) as the

factors for the biochemical data, i.e., the contents of soluble sugars, reducing sugars, sucrose, total phenolic, chlorophylls, and carotenoids in the leaves. When significant effects of damage level on analyzed traits were detected with ANOVA, within each cultivar the control mean (the undamaged leaves) and mean obtained in the damage leaves were compared by Student's *t*-test ($p < 0.05$). The difference between the control (undamaged) leaves and the damaged leaves was recalculated as a percentage of the control value.

To examine the relationship between the number of thrips and the percentage of the damaged leaf area and the sugars and total phenolic contents and some parameters of the leaf's epidermal and mesophyll cells, Pearson's correlation coefficient (*r*) was calculated; significance was set to $p < 0.05$.

3. Results

3.1. Field Resistance Assessment

Onion thrips population sizes were higher in 2015 than in 2016 when the July and August average temperatures were higher and the total rainfall was lower, which likely contributed to the greater thrips infestation in 2015 (Figures 1a–f and S1).

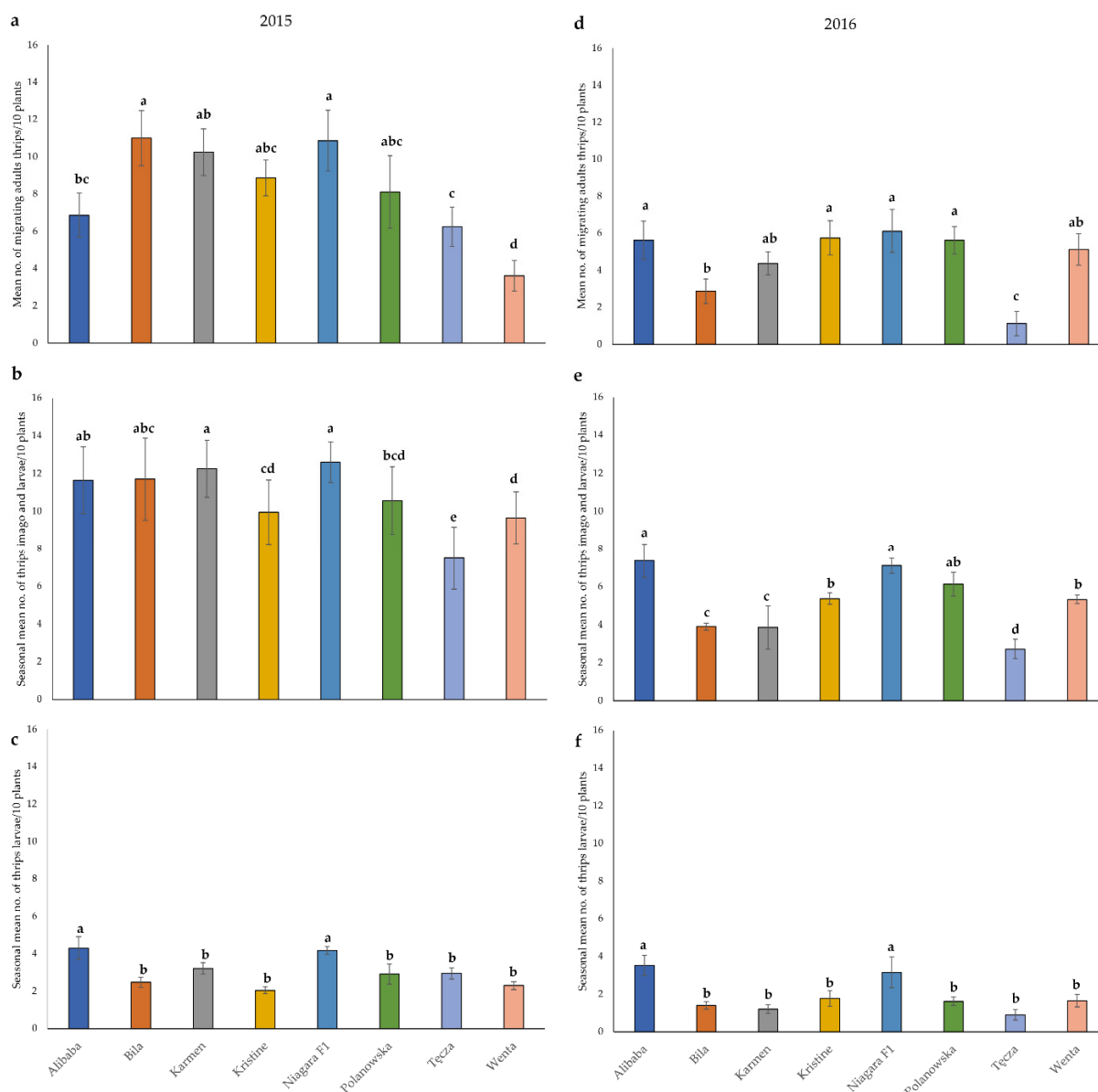


Figure 1. Mean (\pm SE) *Thrips tabaci* abundance on onion cultivars: (a,d) during onion plants colonization by the adults, (b,e) throughout the growing season by adults and larvae, and (c,f) by larvae

of thrips in 2015 and 2016. Means with the same letters on each bar do not differ significantly (Duncan's multiple range Test, $p < 0.05$).

In both years, significant variability of cultivars was found in terms of the mean number of migrating adults of onion thrips, the seasonal mean number of onion thrips imago and larvae, and seasonal mean number of thrips larvae ($p < 0.05$). The block had no significant effect on the seasonal mean number of thrips larvae ($p = 0.475$) in 2015, while in 2016, this factor significantly affected the mean number of migrating adult thrips ($p < 0.05$) (Table S1).

For the year 2015, significantly more migrating adults of onion thrips infested cv. Bila and Niagara F₁ than the other onion cultivars, except for Karmen, Kristine, and Polanowska. Cv. Wenta was infested with the lowest number of adult thrips during onion plants colonization, followed by Tęcza and Alibaba (Figure 1a). A significantly higher seasonal a mean number of onion thrips adults and larvae throughout the growing season was detected on Karmen and Niagara F₁ in comparison with the other cultivars, except for Alibaba and Bila. Cv. Tęcza was infested with the lowest number of onion thrips, followed by Wenta and Kristine (Figure 1b). Onion thrips larvae were less abundant than adults on all onion cultivars. Larvae accounted for 20.6–40.4% of total mean thrips per 10 leaves and values varied by onion cultivar. A significantly higher seasonal mean number of thrips larvae was detected on Alibaba and Niagara F₁ in comparison with the other cultivars (Figure 1c).

The factorial analyses indicated significant differences in the number of thrips sampled on the different cultivars on most of the sampling dates (Table S2). In late June, two cultivars Tęcza and Wenta were not found to be infested by onion thrips, and in early July pest density was significantly lower on Tęcza, Alibaba, and Wenta in comparison to other cultivars. In July and August, the number of thrips was usually significantly lower on Kristine, Tęcza, and Wenta than on other cultivars (Figure S2).

The mean percentage of damaged leaf area showed significant differences between onion cultivars in terms of susceptibility to thrips damage. There was no block effect on this parameter ($p = 0.530$) (Table S1). Cv. Polanowska was significantly the most susceptible to thrips damage than all other cultivars with exception of Tęcza, while the most resistant was Wenta followed by Alibaba, Niagara F₁, Bila, and Karmen (Figure 2a).

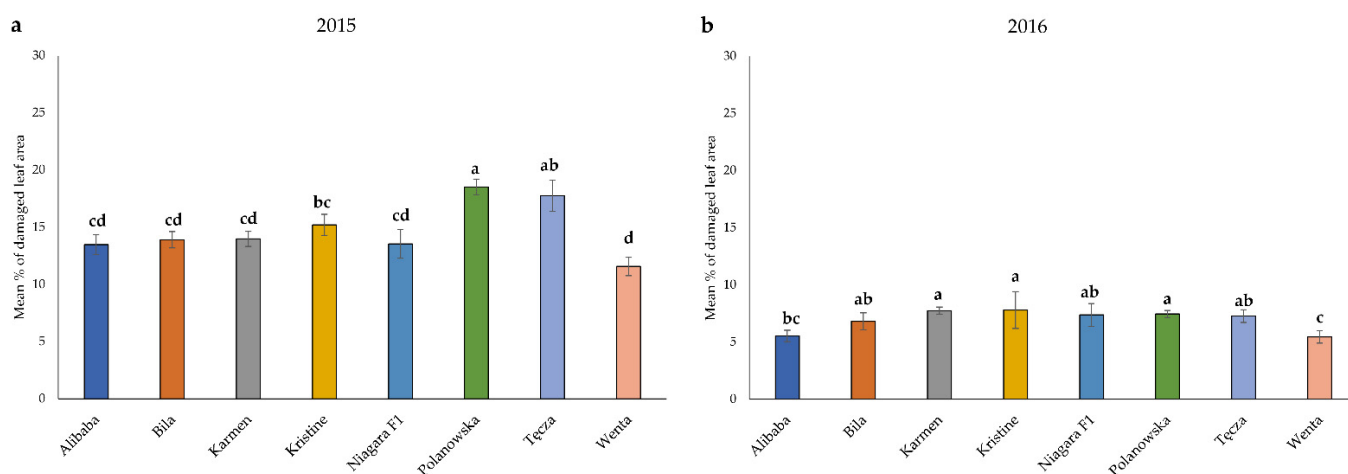


Figure 2. Mean (\pm SE) percentage of the damaged leaf area caused by feeding thrips throughout the all growing season (a) in 2015 and (b) in 2016. Means with the same letters on each bar are do not differ significantly different (Duncan's multiple range Test, $p < 0.05$).

Despite the fact that according to the statistical analysis, the difference between the percentage of damaged leaf area on the eight onion cultivars was significant only for four of the nine sampling events, it seems that in almost all sampling events Polanowska and

Tęcza were the most damaged and Wenta the least damaged in comparison to those others cultivars (Figure S3, Table S2).

For the year 2016, the mean number of adults onion thrips during onion plants colonization was the highest—by a significant margin—on Alibaba, Kristine, Niagara F₁, and Polanowska in comparison with the least colonized (Tęcza), followed by Bila (Figure 1d). A significantly higher seasonal mean number of thrips adults and larvae throughout the whole growing season was detected on Alibaba and Niagara F₁ than on the other cultivars, except for Polanowska. Kristine and Wenta fell into the second homogenous group when Duncan's test was performed, while Bila and Tęcza fell into the third and fourth groups, respectively (Figure 1e). The larvae accounted for 26.5–47.8% of total mean thrips per 10 leaves and a significantly higher seasonal mean number of thrips larvae was detected on Alibaba and Niagara F₁ in comparison with the other cultivars (Figure 1f).

The factorial analyses indicated highly significant differences in the number of thrips sampled on the different cultivars on most of the sampling dates (Table S2). Onion thrips population density was usually significantly higher on Alibaba, Niagara F₁, and Polanowska than on Bila, Karmen, and Tęcza (Figure S4).

Significant variability of cultivars was found in terms of the mean percentage of damaged leaf area caused by feeding thrips. There was a block effect for this parameter ($p = 0.049$) (Table S1). The mean percentage of damaged leaf area was significantly the highest on Karmen, Kristine, and Polanowska in comparison to less susceptible to thrips feeding Alibaba and resistant Wenta (Figure 2b).

The factorial analyses indicated significant differences in the percentage of damaged leaf area sampled on the different cultivars on 7 July with significantly most damaged cv. Tęcza in comparison to others, and on the two last sampling dates in August with significantly the most damaged (Karmen and Polanowska) and significantly the least damaged (Alibaba and Wenta) (Figure S5, Table S2).

Based on these results, two cultivars with field resistance to thrips abundance were identified: Tęcza and Wenta, one cultivar resistant to thrips feeding: Wenta, five susceptible: Alibaba, Bila, Karmen, Kristine, and Polanowska, and one highly susceptible: Niagara F₁. All these susceptible cultivars were the most attractive to adult onion thrips for colonization, with Niagara F₁ better supporting the thrips infestation during the migration period. Two cultivars Tęcza and Wenta were resistant and moderately resistant to migrating adult thrips, respectively (Table 2).

Table 2. Level of resistance of eight onion cultivars to *Thrips tabaci*.

Cultivars	Resistance to		Field Resistance Throughout the Growing Season			
	Plant Colonization		Resistance to		Resistance to	
	by Migrating Adult Thrips		Thrips Abundance		Thrips Damage	
	No. Points	Level of Resistance	No. Points	Level of Resistance	No. Points	Level of Resistance
Alibaba	1.5	susceptible	1.5	susceptible	2.0	susceptible
Bila	2.0	susceptible	2.5	susceptible	2.0	susceptible
Karmen	1.5	susceptible	2.0	susceptible	1.5	susceptible
Kristine	1.5	susceptible	2.5	susceptible	1.5	susceptible
Niagara F ₁	1.0	High susceptible	1.0	high susceptible	1.5	susceptible
Polanowska	1.5	susceptible	2.0	susceptible	1.0	high susceptible
Tęcza	3.5	resistant	4.0	resistant	1.5	susceptible
Wenta	3.0	Moderately resistant	2.5	Moderately resistant	4.0	resistant

Note: the level of resistance: >3.00 points—resistant; 3.00–2.50 points—moderately resistant; 2.49–1.5 points—susceptible; <1.5 points—high susceptible.

3.2. Biochemical Bases of Resistance

In both 2015 and 2016, there was a significant effect of variety ($p < 0.05$) on the contents of soluble and reducing sugars, sucrose, and total phenolics in the undamaged leaves by feeding onion thrips of onion cultivars, and there was no block effect only on concentrations of sucrose in 2015 and total phenolics in both years (Tables 3 and 4).

Table 3. The contents of sugars and total phenols in the not damaged by *Thrips tabaci* leaves of the onion cultivars in 2015, $df = 7$.

Cultivar	Mean Quantity (\pm SE) (mg/100 g FW ¹)			
	Soluble Sugars	Reducing Sugars	Sucrose	Total Phenols
Alibaba	1.25 \pm 0.012 b ²	0.125 \pm 0.012 a	1.13 \pm 0.004 b	97.23 \pm 1.24 b
Bila	0.91 \pm 0.024 e	0.077 \pm 0.003 bc	0.84 \pm 0.021 e	72.63 \pm 0.33 d
Karmen	1.13 \pm 0.002 c	0.084 \pm 0.001 b	1.04 \pm 0.002 c	74.85 \pm 0.15 d
Kristine	0.91 \pm 0.002 e	0.067 \pm 0.007 c	0.85 \pm 0.002 e	64.75 \pm 0.88 d
Niagara F ₁	1.15 \pm 0.002 c	0.124 \pm 0.008 a	1.02 \pm 0.006 c	81.50 \pm 0.62 c
Polanowska	0.86 \pm 0.007 f	0.074 \pm 0.001 bc	0.78 \pm 0.006 f	73.24 \pm 0.43 d
Tęcza	1.05 \pm 0.007 d	0.079 \pm 0.002 b	0.97 \pm 0.005 d	68.08 \pm 0.85 d
Wenta	1.35 \pm 0.008 a	0.077 \pm 0.006 bc	1.27 \pm 0.004 a	99.93 \pm 1.37 a
<i>p</i> cultivar	<0.001	<0.001	<0.001	<0.001
F blocks	8.6	11.657	1.9	0.58
<i>p</i> blocks	<0.001	<0.001	0.156	0.636

Note: ¹FW = Fresh weight; ² means within a column followed by the same letter(s) do not differ significantly (Duncan's Multiple Range Test $p < 0.05$).

Table 4. The contents of sugars and total phenols in the not damaged by *Thrips tabaci* leaves of the tested onion cultivars in 2016, $df = 7$.

Cultivar	Mean Quantity (\pm SE) (mg/100 g FW ¹)			
	Soluble Sugars	Reducing Sugars	Sucrose	Total Phenols
Alibaba	1.17 \pm 0.011 b ²	0.13 \pm 0.001 a	1.04 \pm 0.010 c	74.82 \pm 1.23 a
Bila	0.96 \pm 0.009 f	0.10 \pm 0.001 c	0.87 \pm 0.008 f	54.83 \pm 0.27 d
Karmen	1.19 \pm 0.016 b	0.09 \pm 0.003 d	1.10 \pm 0.014 b	57.92 \pm 0.30 c
Kristine	0.94 \pm 0.028 f	0.05 \pm 0.004 f	0.88 \pm 0.024 f	47.91 \pm 0.54 d
Niagara F ₁	1.09 \pm 0.010 c	0.11 \pm 0.001 b	0.97 \pm 0.009 d	67.55 \pm 0.68 b
Polanowska	1.37 \pm 0.014 a	0.12 \pm 0.002 b	1.25 \pm 0.013 a	49.69 \pm 0.70 d
Tęcza	1.03 \pm 0.08 d	0.10 \pm 0.001 c	0.93 \pm 0.007 e	76.26 \pm 0.69 a
Wenta	1.09 \pm 0.019 e	0.08 \pm 0.003 e	0.92 \pm 0.016 e	75.86 \pm 1.87 a
<i>p</i> cultivar	<0.001	<0.001	<0.001	<0.001
F blocks	16.3	9.12	15.5	0.77
<i>p</i> blocks	<0.001	<0.001	0.005	0.523

Note: ¹FW = Fresh weight; ² means within a column followed by the same letter(s) do not differ significantly (Duncan's Multiple Range Test $p < 0.05$).

In 2015, most onion cultivars differed significantly from each other in terms of contents of soluble sugars and sucrose in leaves, and only Karmen with Niagara F₁ and Bila with Kristine fall into the same homogenous groups when the Duncan test was performed (Table 3). The highest mean quantity of soluble sugars and sucrose in leaves was shown by cv. Wenta, a cultivar resistant to thrips damage, while the lowest concentrations of both carbohydrates were shown by a cultivar susceptible to thrips abundance and thrips damage, namely cv. Polanowska. The sequence of other cultivars in terms of contents of soluble sugars and sucrose was the same for both carbohydrates (Table 3). The cultivar found to be second most susceptible to thrips damage in 2015 (cv. Tęcza) was placed at the end

of the list in terms of the contents of soluble sugars and sucrose and contained carbohydrates in average concentrations compared to other cultivars (Table 3). Significantly, the highest quantity of reducing sugars was found in the leaves of the cultivars Alibaba and Niagara F₁ with a high density of thrips, but moderately damaged leaves in 2015 (Table 3). A cultivar susceptible to thrips damage (cv. Kristine) contained the lowest concentration of reducing sugars, but it did not significantly differ from the quantity thereof in the leaves of Bila and Wenta, which had a lower percentage of damaged leaf area (Table 3).

For the total phenolic contents, Duncan's test produced four homogenous groups (Table 3). Cv. Wenta, which was resistant to thrips abundance and thrips damage in 2015, had the highest mean quantity of total phenolics. Cultivars Alibaba and Niagara F₁ fell into the second and third group, respectively, while the five other cultivars formed the fourth group, with the lowest quantity of total phenolics in leaves of cv. Kristine (Table 3).

In 2016, in contrast to the previous year, one of the cultivars most infested and damaged by onion thrips (cv. Polanowska) showed the highest mean quantity of soluble sugars and sucrose, while the lowest concentrations of these carbohydrates were shown by a cultivar susceptible especially to thrips damage (cv. Kristine), followed by cv. Bila (Table 4). The highest level of reducing sugars was shown by a cultivar mainly susceptible to thrips abundance (cv. Alibaba) and then two cultivars susceptible to thrips abundance and damage, namely, Niagara F₁ and Polanowska, while the lowest was detected in the leaves of Wenta (Table 4).

In 2016, the significantly highest phenolic content was found in the leaves of Tęcza, Alibaba, and Wenta, and these cultivars were characterized by high, medium, and low degrees of leaf damage, respectively. The lowest concentrations of these chemical compounds were detected in the leaves of cultivars susceptible to thrips damage, i.e., Bila, Kristine, and Polanowska (Table 4).

In 2015, the content of reducing sugars in the undamaged leaves of onion cultivars was positively correlated with the mean number of thrips on 28 July (when the leaves were sampled for biochemical analyses) and with the seasonal mean number of thrips. In turn, the concentrations of total soluble sugars, sucrose, and total phenolics correlated negatively with the seasonal mean percentage of damaged leaf area (Table 5).

Table 5. Pearson's correlation between biochemical characteristics of onion leaves and the number of *Thrips tabaci* and percentage of damaged leaf area of onion leaves in 2015 ($n = 32$).

Parameters	No. of Thrips (Imago + Larvae)				Damaged Leaf Area			
	Mean No. of Thrips on 28 July		Seasonal Mean No. of Thrips		Mean Percentage of Damaged Leaf Area on 28 July		Seasonal Mean Percentage of Damaged Leaf Area	
	r	p	r	p	r	p	r	p
Mean quantity of total soluble sugars (g/100 ⁻¹ g FW)	0.026	0.146	0.115	0.530	-0.305	0.089	-0.589 *	0.000
Mean quantity of reducing sugars (g/100 ⁻¹ g FW)	0.579*	0.001	0.489 *	0.004	-0.216	0.234	-0.281	0.120
Mean quantity of sucrose (g/100 ⁻¹ g FW)	0.194	0.287	0.051	0.785	-0.293	0.104	-0.586 *	0.000
Mean total phenols contents (mg/100 ⁻¹ g FW)	0.313	0.081	0.082	0.655	-0.253	0.162	-0.534 *	0.002

Note: * - significant correlation at $p < 0.05$.

For the year 2016, the correlation coefficient indicated that there was a positive correlation between three carbohydrates and the mean number of thrips on 8 August (when the leaves were sampled for biochemical analyses) and between the level of reducing sugars and the seasonal mean number of thrips. On the contrary, a negative significant correlation was detected between the concentration of total phenols and the mean percentage of damaged leaf area on 8 August and throughout the whole growing season (Table 6).

Table 6. Pearson's correlation between biochemical characteristics of onion leaves and the number of *Thrips tabaci* and percentage of damaged leaf area of onion leaves in 2016 ($n = 32$).

Parameters	No. of Thrips (Imago + Larvae)				Damaged Leaf Area			
	Mean No. of Thrips on 8 August		Seasonal Mean No. of Thrips		Mean Percentage of Damaged Leaf Area on 8 August		Seasonal Mean Percentage of Damaged Leaf Area	
	r	p	r	p	r	p	r	p
Mean quantity of total sugars (g/100 ⁻¹ g FW)	0.523 *	0.002	0.319	0.075	0.081	0.655	0.598	0.745
Mean quantity of reducing sugars (g/100 ⁻¹ g FW)	0.395 *	0.025	0.397 *	0.024	-0.120	0.513	-0.246	0.175
Mean quantity of sucrose (g/100 ⁻¹ g FW)	0.508 *	0.003	0.282	0.118	0.112	0.543	0.110	0.548
Mean total phenols contents (mg/100 ⁻¹ g FW)	-0.124	0.500	0.411	0.823	-0.390 *	0.027	-0.421 *	0.016

Note: * - significant correlation at $p < 0.05$.

3.3. Anatomical Characters of Leaves

In the onion cultivars examined in 2016, the leaf blade thickness was a significantly varying trait (Table 7). It was found that cultivars Alibaba and Karmen had the thickest leaf blades, while the thinnest leaf blades were found for Polanowska, followed by Wenta (Table 7).

Table 7. Leaf blade thickness of the tested *Alium cepa* cultivars in 2016, $df = 7$.

Cultivar	Max. Leaf Blade Thickness (Mean \pm SE) (μm)	Min. Leaf Blade Thickness (Mean \pm SE) (μm)	Mean Leaf Blade Thickness (Mean \pm SE) (μm)
Alibaba	528.6 \pm 6.84 c ¹	520.6 \pm 6.86 a	524.6 \pm 6.74 a
Bila	495.4 \pm 2.73 d	347.0 \pm 5.63 e	421.2 \pm 2.73 d
Karmen	598.4 \pm 5.71 a	432.0 \pm 3.66 b	515.2 \pm 2.72 a
Kristine	566.0 \pm 7.44 b	409.6 \pm 27.51 bc	487.8 \pm 17.24 b
Niagara F ₁	451.6 \pm 3.53 e	376.4 \pm 5.45 cd	414.0 \pm 2.24 d
Polanowska	385.0 \pm 4.37 g	367.2 \pm 2.17 de	376.1 \pm 2.35 f
Tęcza	503.8 \pm 3.55 d	403.6 \pm 4.74 bc	453.7 \pm 2.78 c
Wenta	435.2 \pm 3.68 f	357.8 \pm 4.29 de	396.5 \pm 2.21 e
F cultivar	217.00	25.3	77.0
p cultivar	<0.001	<0.001	<0.001

Note: ¹ means within a column followed by the same letter(s) do not differ significantly (Duncan's Multiple Range Test $p < 0.05$).

The thickness of the epidermis, perimeter, and area of the epidermal cells, as well as mesophyll cells were significantly affected by onion cultivars ($p < 0.05$) (Table 8).

Table 8. The evaluated parameters of the leaf's epidermal and mesophyll cells in evaluated eight different *Allium cepa* cultivars in 2016, df = 7.

Cultivar	Epidermis			Cell Layers (No)	Mesophyll	
	Mean (\pm SE)				Mean (\pm SE)	
	Thickness (μ m)	Perimeter (μ m)	Area (μ m ²)		Perimeter (μ m)	Area (μ m ²)
Alibaba	25.65 \pm 0.96 b ¹	84.23 \pm 9.70 c	482.06 \pm 26.26 c	7	115.98 \pm 10.51 e	734.04 \pm 131.19 d
Bila	27.38 \pm 0.79 ab	100.33 \pm 15.01 ab	654.24 \pm 35.99 ab	8	208.85 \pm 12.39 a	1579.52 \pm 151.44 abc
Karmen	27.61 \pm 1.07 ab	96.50 \pm 18.58 b	615.49 \pm 43.88 bc	7	194.89 \pm 9.19 ab	1652.59 \pm 116.56 a
Kristine	29.95 \pm 0.65 a	107.78 \pm 9.22 a	775.38 \pm 26.19 a	6	192.20 \pm 14.23 abc	1780.38 \pm 198.65 ab
Niagara F ₁	26.28 \pm 0.97 b	93.77 \pm 11.26 b	568.00 \pm 31.80 bc	6	152.49 \pm 15.42 cde	1121.54 \pm 168.21 bc
Polanowska	26.08 \pm 1.56 b	108.15 \pm 18.40 a	789.77 \pm 68.38 a	7	140.02 \pm 15.94 cd	1084.48 \pm 171.63 cd
Teęza	25.38 \pm 1.01 b	99.88 \pm 18.50 ab	687.90 \pm 52.03 ab	6	166.41 \pm 11.31 abcd	1480.72 \pm 156.18 abc
Wenta	24.28 \pm 1.10 b	95.23 \pm 17.20 b	594.28 \pm 46.91 bc	8	153.72 \pm 11.10 bcd	1142.13 \pm 140.64 abc
F cultivar	3.17	4.70	4.71		4.88	4.34
p cultivar	0.004	<0.001	<0.001		<0.001	<0.001

Note: ¹ means within a column followed by the same letter(s) do not differ significantly (Duncan's Multiple Range Test $p < 0.05$).

For the thickness of the epidermis, Duncan's test gave two homogenous groups. Cv. Kristine, which was the most damaged by onion thrips in 2016, had the thickest epidermis layer and fell into the first group, while three cultivars susceptible to thrips damage, namely Niagara F₁, Polanowska, Teęza as well as moderately resistant Alibaba and resistant Wenta, were placed into the second group. The mean thickness of the epidermis of two susceptible cultivars Bila and Karmen did not differ significantly from other cultivars (Table 8, Figure 2b). The leaf blades of Alibaba, Karmen, and Wenta were characterized by the smallest perimeter and area of epidermal cells in comparison with Kristine and Polanowska (differing significantly). Alibaba also showed smaller mesophyll cells in comparison to other onion cultivars; their perimeter and area proved to be significantly smaller than in other cultivars, except for the area of the mesophyll cells of cv. Polanowska (Table 8). Analyzed material had a similar number of cell layers in the mesophyll (about 6–8 layers). A leaf anatomical study revealed that vascular bundles (VB) were arranged in one row. There was a cultivar effect only on the mean distance between them and the largest values were noted between VB of Alibaba in comparison to others, except for Bila and Karmen (Table 9). The smallest distance between VB was detected in the leaves of Polanowska but it did not differ statistically from that of Kristine, Niagara F₁, Teęza, and Wenta (Table 9). Despite the lack of significant differences between the mean diameter, perimeter, and cross-sectional area of vascular bundles of the tested onion cultivars, the smallest mean perimeter and mean cross-sectional area were found in the leaves of cv. Wenta, which was the least damaged by thrips in 2016, while the largest was found in Bila and Karmen, which were highly damaged by these pests (Table 9).

Table 9. The evaluated parameters of vascular bundles (VB) in leaves of evaluated eight different *Allium cepa* cultivars in 2016, df = 7.

Cultivar	Mean Diameter (±SE) (µm)	Mean Perimeter (±SE) (µm)	Mean Cross-Section Area (±SE) (µm ²)	Mean Distance Between VB (±SE) (µm)
Alibaba	156.67 ± 9.95	478.00 ± 12.16	13077.33 ± 418.41	>1000.00 a ¹
Bila	118.33 ± 19.01	594.67 ± 101.13	17144.00 ± 5637.38	831.68 ± 88.52 ab
Karmen	170.00 ± 57.41	504.00 ± 153.13	16817.67 ± 7145.38	744.33 ± 128.19 abc
Kristine	154.67 ± 40.68	470.00 ± 103.92	12752.00 ± 3995.18	438.00 ± 22.19 bcd
Niagara F ₁	53.00 ± 3.51	289.00 ± 46.36	4836.67 ± 1573.59	347.67 ± 10.82 cd
Polanowska	76.67 ± 12.17	241.00 ± 30.80	3936.00 ± 1000.16	264.33 ± 65.46 d
Tezca	116.67 ± 52.44	343.66 ± 134.55	7752.33 ± 5078.374	496.00 ± 252.68 cd
Wenta	60.00 ± 19.03	212.67 ± 68.91	3059.33 ± 1945.752	454.00 ± 112.01 bcd
F cultivar	2.191	2.146	2.164	4.587
p cultivar	0.092	0.098	0.095	0.005

Note: ¹ means within a column followed by the same letter(s) do not differ significantly (Duncan's Multiple Range Test $p < 0.05$).

The phloem part of the vascular bundles was oriented to the upper leaf surface. Therefore, it is of significance how deeply the collateral bundles lie in the leaf mesophyll and this feature is directly related to the thickness of the leaf blade. The leaf blades lacked a clear palisade mesophyll evolved secondarily from spongy ones.

The correlation coefficient of anatomical parameters of onion leaves indicated that there was a significant correlation among the three variables. To simplify the coverage of the results, the significant correlations are included in the main text while the results of all computed interactions are included in Table S3. The mean area of mesophyll cells correlated negatively with the seasonal mean number of thrips ($r = -0.734$, $p = 0.038$), as well as the mean perimeter of vascular bundles with the seasonal mean number of thrips and the mean number of thrips observed on plants 8 August ($r = -0.710$, $p = 0.048$), when onion leaves were sampled for anatomical studies. On the contrary, the mean area of mesophyll cells was positively correlated with an increasing percentage of damaged leaf area detected on 8 August ($r = 0.738$, $p = 0.036$).

3.4. Effect of Mechanical Injury Caused by Feeding Onion Thrips on the Concentration of Carbohydrates, Total Phenolics, and Leaf Pigments Contents in Onion Leaves

Total soluble sugars, reducing sugars, sucrose, and total phenolic contents in the undamaged onion leaves in 2015 and 2016 are presented in Tables 3 and 4, respectively, while in damaged leaves by feeding thrips is shown in Tables S4 and S5. In both years, there was a significant effect of the cultivar ($p < 0.05$) on contents of soluble and reducing sugars, sucrose, and total phenolics in the damaged leaves of onion cultivars, and there was no block effect on concentrations of sucrose and total phenolics in 2015 and total phenolics in 2016 (Tables S4 and S5).

Chlorophyll a and b and total carotenoid contents in undamaged and damaged onion leaves are presented in Tables S6 and S7. In both years, there was a significant effect of the variety ($p < 0.05$) on contents of chlorophyll a and b, and sum of carotenoids in undamaged and damaged leaves of onion cultivars, and there was no block effect only on concentrations of chlorophyll b and a sum of carotenoids in damaged leaves in 2015 (Tables S6 and S7).

Two-way ANOVA analysis showed significant differentiation in the size of cultivar and damage level in terms of the analyzed biochemical parameters of onion leaves (Table S8).

In the leaves of onion plants which were not damaged by the onion thrips, the contents of total soluble sugars and sucrose were significantly higher than in damaged leaves in all onion cultivars, in both 2015 and 2016 (Figure 3a,c,e,g).

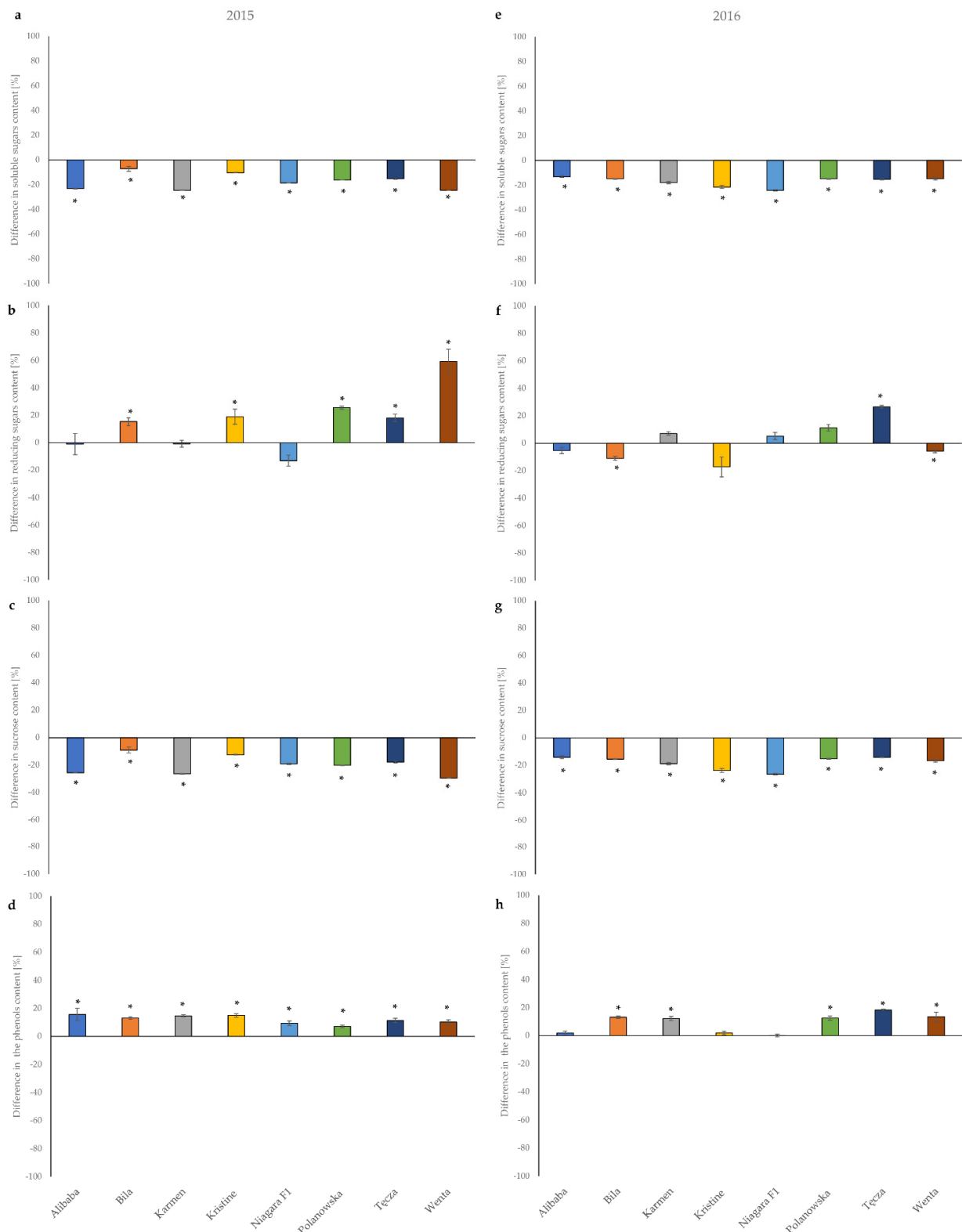


Figure 3. Effects of *Thrips tabaci* foraging on contents of (a,e) soluble sugars, (b,f) reducing sugars, (c,g) sucrose, (d,h) total phenols in the leaves of tested onion cultivars in 2015 and 2016. * - significant differences between the control mean and the mean in colonized plants based on the Student's *t*-test conducted separately for each cultivar ($p < 0.05$).

The highest decrease in the concentration of soluble sugars and sucrose (>20%) was recorded for Alibaba, Karmen, and Wenta in 2015 (Figure 3a) and Kristine and Niagara F₁ in 2016 (Figure 3e), while the smallest decrease was observed (<10.3%) for Bila and Kristine in 2015

(Figure 3a). Furthermore, a high decrease in sucrose concentration (>20%) was observed in the leaves of Polanowska and Niagara F1 in 2015 (Figure 3c). In 2015, Alibaba, Karmen, and Niagara F1 did not respond to the feeding of the onion thrips with significant changes in the concentration of reducing sugars (Figure 1b). In that year, thrips caused the highest significant increase in the concentrations of reducing sugars in damaged leaves of Wenta (>50%) and Bila, Tęcza, Kristine, and Polanowska (from 15.33% to 25.56%) (Figure 3b). In 2016, Tęcza responded to the feeding of the thrips with a significant increase in the concentration of reducing sugars, while in the case of the Bila and Wenta opposite responses were recorded (Figure 3f).

The concentrations of total phenolics in leaves damaged by feeding onion thrips were significantly higher than in undamaged leaves in all onion cultivars in 2015, and—in the case of Bila, Karmen, Polanowska, Tęcza, and Wenta—also in 2016. All of these cultivars, except for Niagara F1 and Polanowska in 2015, reacted to thrips feeding with an increase in the of total phenols contents above 10% (Figure 3d,h).

In 2015, all onion cultivars responded to the feeding of onion thrips with a decrease in the contents of all tested leaf pigments, but this result was significant only in the case of five onion cultivars: Bila, Karmen, Kristine, Polanowska, and Tęcza in terms of chlorophyll a; three cultivars; Kristine, Niagara F1, and Wenta in terms of chlorophyll b; and two cultivars: Bila and Wenta in terms of total carotenoids. The highest decrease, of more than 10%, was observed for the content of chlorophyll b (Figure 4a–c).

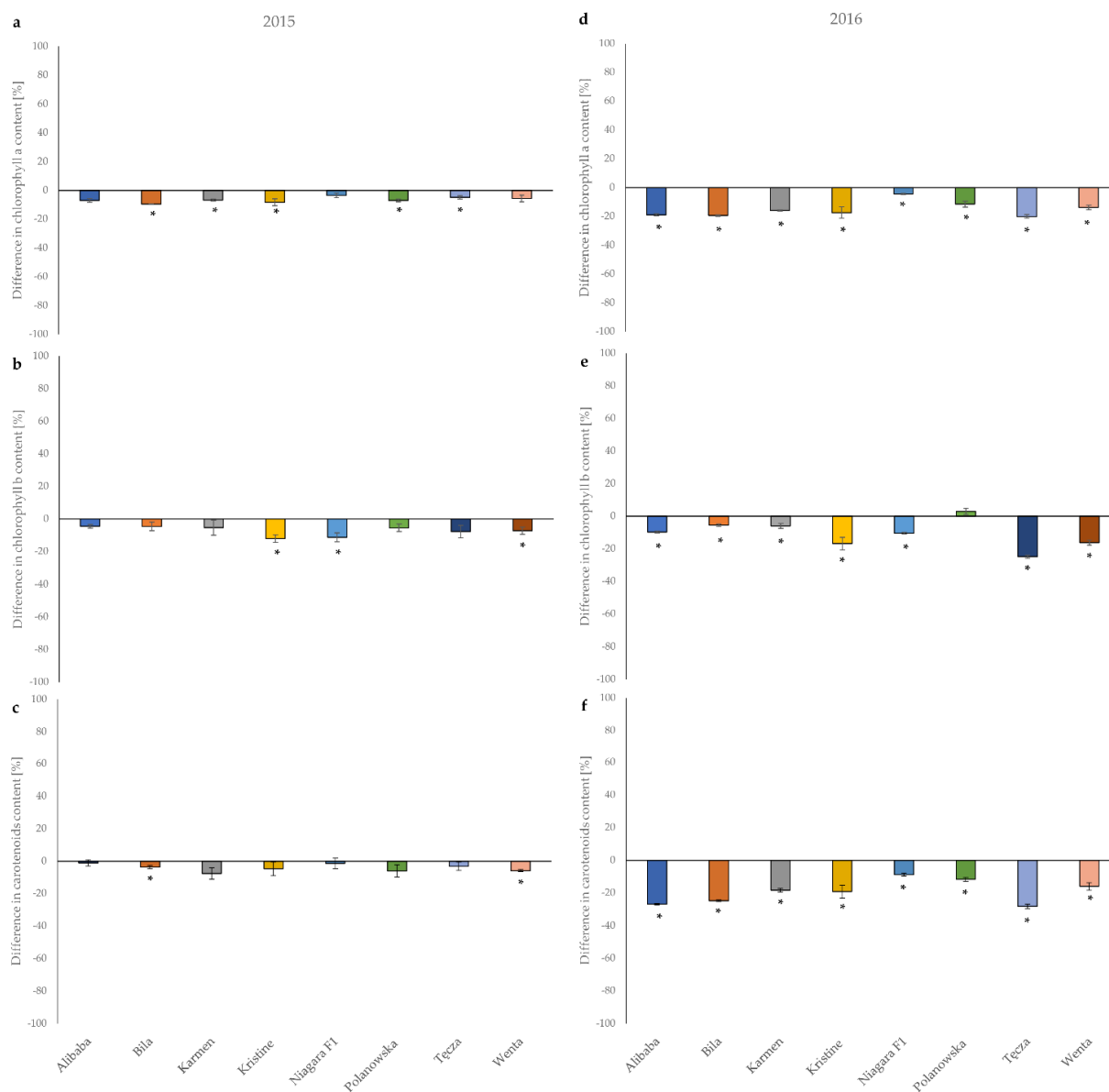


Figure 4. Effects of *Thrips tabaci* foraging on contents of (a,d) chlorophyll a, (b,e) chlorophyll b, and (c,f) carotenoids in the leaves of tested onion cultivars in 2015 and 2016. * - significant differences between the control mean and the mean in colonized plants based on the Student's *t*-test conducted separately for each cultivar ($p < 0.05$).

In 2016, thrips feeding caused a significant decrease in the concentrations of chlorophyll a and b and total carotenoids in leaves of all onion cultivars with the exception of chlorophyll b in the case of Polanowska. The highest reduction of all leaf pigments (>20%) was detected in the leaves of cv. Tęcza (Figure 4d–f).

4. Discussion

In the field experiment, two cultivars Tęcza and Wenta were moderately resistant and resistant, respectively, to onion thrips as reflected in the lower thrips population and/or low percentage of damaged leaf area by feeding thrips observed throughout the growing season. Nevertheless, because the experiment involved both mechanisms (antixenosis, antibiosis), attempts to apportion one (or both) of those mechanisms () as the factor contributing most significantly to the observed difference in the level of overall pest resistance are inherently difficult. Antixenosis testing is mainly based on measuring the attractiveness of a plant genotype to colonizers and is an important component of resistance because it reduces the initial infestation level [52]. In our experiment, the weak colonization of cultivars Tęcza and Wenta by migrating adult thrips may indicate host plant selection and the antixenotic (no preference) mechanism of resistance of these cultivars. Antixenosis has been documented in onion and cabbage for onion thrips and some of the plant characteristics that are perceivable before landings, such as the size, shape, and scent of the host plant, as well as colour and light reflectance of leaves have been involved in this mechanism [26–28,53,54]. Moreover, differences in foliar reflectance of light could be due to differences in profiles of cuticular waxes between resistant and susceptible cultivars [13,26,37]. As mentioned in the introduction, onion cultivars with glossy and light yellow-green foliage support a lower number of onion thrips and suffer less feeding damage in comparison with nonglossy (waxy) and blue-green susceptible cultivars [26,36]. However, a lighter leaf colour of onion accessions and/or a lesser amount of epicuticular wax did not always result in the fewest number of thrips per plant [55]. It is supposed that a decreased amount of cuticular wax in resistant onion varieties suppresses thrips feeding on leaves to a greater degree than onion colonization by them because the wax layer allows them to adhere to the plant and cause damage [36,55]. On the contrary, Eigenbrode et al. [56] found that on cabbage leaves, a high quantity of wax hinders the movement of small insects probably by means of wax crystals accumulating on the tarsi. A negative relationship between the amount of epicuticular waxes and the densities of thrips and damage caused by them in cabbage plants was reported by Trdan et al. [57] and Voorrips et al. [58]. In our study, onion cultivars resistant to migrating thrips settlement (Wenta and Tęcza) stood out among other varieties due to their darker, green-grey-yellowish leaf color, while susceptible cultivars had the vivid, intense green-yellowish color of chives [42]. Colour characteristics of leaves of tested onion cultivars have been described in detail in the earlier work of Pobożniak et al. [42], while the amount and composition of the epicuticular wax have not been identified so far.

The lower values of thrips abundance obtained from field tests on the cultivars Tęcza and Wenta throughout both growing seasons and cultivars Kristine in 2015 and Bila and Karmen in 2016 indicate that the onion thrips population did not reach a high abundance, which could be due to them not being able to successfully build up large populations on these cultivars under natural conditions, which may have resulted from antixenosis during pre-foraging and/or antibiosis during feeding. Field screening of onion cultivars revealed also differences in plant injury caused by thrips feeding between tested cultivars. According to Lewis [59], the method of feeding and the shape and depth of damage left by thrips vary between resistant and susceptible plants. Mollema et al. [60] found that on

susceptible varieties of cucumber, the feeding holes caused by western flower thrips, *Frankliniella occidentalis* Pergande were grouped while on resistant varieties, thrips appeared restless, spent most of their time walking, and the feeding holes were scattered individually. In both years of our study, fewer and scattered traces of foraging by onion thrips were observed on the leaves of cv. Wenta, although this cultivar was subject to the pressure of a similar pest population as the more extensively damaged cultivars Kristine and Polanowska. In turn, cv. Tęcza possessed fewer thrips per plant than other cultivars, but a percentage of the damaged leaf area on it was comparable to those on cultivars susceptible to thrips damage like Polanowska (in both years) and Niagara F₁, Karmen, and Kristine in 2016. Njau et al. [40] also observed negative (although non-significant) correlations between the number of onion thrips and the mean leaf damage in different onion accessions; Miyazaki et al. [61] reported similar findings in the case of onion thrips, western flower thrips, and cotton thrips, *Frankliniella schultzei* (Trybom) on cotton cultivars. The similarities in the levels of thrips damage among cultivars harboring a different number of thrips, as vividly exemplified by Tęcza and Polanowska, suggest that the resistance to thrips damage and the abundance could be linked to the different specific traits of the onion cultivars.

Primary metabolites such as proteins and carbohydrates are nutrients needed to synthesize body tissue and serve as energy sources, stimulating feeding, and influencing life-history parameters of thrips [29,62]. In studies by Agbahoungba et al. [63], the concentration of total sugars and reducing sugars in the plants of cowpea contributed to the reduction of damage caused by flower bud thrips, *Megalurothrips sjostedti* Trybom. Contradictory findings have been reported by Kandakoor et al. [64] and Chandrayudu et al. [65], who found a positive relationship between the quantity of total sugars and the number of thrips on peanuts. Similarly, Njau et al. [40] and Bhonde et al. [66] found that the total sugars content in leaves of onion accessions was positively correlated with the number of onion thrips, while the authors also reported an inverse (although non-significant) relationship between their concentration and thrips damage. Pobożniak and Koschier [30] and Žnidarčič et al. [67] proved that sucrose contents in the leaves promoted the population growth of the onion thrips on pea and cabbage leaves. In our experiment, the concentrations of soluble sugars and sucrose in the onion leaves were significantly positively correlated with the number of onion thrips (but only in 2016), while for both years the positive correlation between the reducing sugars quantity and thrips density was confirmed. Srinivas et al. [68] and Bhonde et al. [66] also indicated that onion thrips were more attracted to onion plants when they had a high concentration of reducing sugars. The low or moderate level of reducing sugars in the leaves of cultivar Tęcza, resistant to thrips infestation, and cultivars Bila, Kristine, and Wenta with lower thrips density probably could contribute to this resistance. In turn, the increasing concentrations of soluble sugars and sucrose significantly decreased thrips damage only in 2015. This fact, and the highest content of soluble sugars and sucrose in leaves of Wenta in 2015, is likely to be one of the causes of resistance to thrips damage of this variety, although this was not confirmed in the results obtained in 2016.

In addition to sugars, phenolic compounds are also implicated as being involved in conferring resistance to thrips [69]. Phenolic groups of secondary metabolites such as flavonoids, tannins, and related phenolic precursors are widely reported as playing a significant role in defense against insect herbivores [70]. Ahmed et al. [71] and Bhonde et al. [66] indicated that free and bound phenolic contents showed a negative correlation with the number of onion thrips in bread wheat and onion cultivars, respectively. Njau et al. [40] and Akhtari et al. [72] found that phenolic concentrations in onion and Persian leek accessions, respectively, showed a significant adverse effect on onion thrips damage. Kandakoor et al. [64] and Agbahoungba et al. [63] described a similar effect of phenolics content on thrips damage to peanuts. The results obtained in this study confirm the research findings of the above-mentioned authors. It can be suspected that the reason for the resistance of cv. Wenta to thrips damage could be the higher phenolic content in its leaves, compared to other more damaged varieties. The difference in the degree of leaf damage between cultivars harboring thrips populations of similar density, as exemplified by

Wenta and Kristine, could be explained at least partially by the fact that Wenta had the highest concentrations of total phenols in the leaves, while Kristine had the lowest. The low quantity of phenolics in the cv. Tęcza leaves in 2015 could also explain its high susceptibility to thrips damage in that year. However, it is not clear why the higher level of phenolic content in the leaves of this variety in 2016 did not significantly reduce the degree of its damage in that year.

Plant phenolic compounds are accumulated in the vacuoles and kept reduced by antioxidants [73]. After plant cells are ingested by thrips, the released phenolic compounds become susceptible to autooxidation or are oxidized by salivary oxidases, as in the case of aphids [73]. Plant phenols are often bitter in taste, which effectively protects plants against herbivores. Others may act as a chemical defense due to the prooxidative effect of some of their derivatives; e.g., chlorogenic acid is oxidized to chlorogenoquinone, which, by binding to free amino acids and proteins, reduces the bioavailability of amino acids and hinders the digestion of food proteins [74]. This negative effect of this compound on western flower thrips and aphids has been detected by Leiss et al. [75] and Miles and Oertli [76], respectively. Phenolics are also known for their role in plant defense by mechanically hindering the feeding of insects with piercing–sucking mouthparts. Feruloyl quinic acid is a precursor of lignin, conferring rigidity to cell walls, which has been linked to resistance to cereal aphids [77]. In conclusion, we state that the correlative roles of phenolic compounds in thrips resistance should be characterized further by isolating these compounds from the onion germplasm and conducting bioassays with onion thrips. Moreover, the effect of phenolic compounds on herbivores will also depend on their quantity in the plant tissue.

Thrips feeding can also induce the build-up of total phenolic contents in onion, as documented by Srinivas et al. [68]. According to Ananthakrishnan et al. [78], increased production of phenolics and alterations in the composition of phenolic acids and flavonoids in castor and eucalyptus as responses to infestations of black wine thrips, *Retithrips syriacus* (Mayet) can be considered manifestations of induced resistance. We also reported an increase in concentrations of total phenolic content in leaves damaged by onion thrips. Perhaps the weaker increase in the phenolic contents in the leaves of Polanowska (in 2015) and Kristine and Niagara F₁ (in 2016) reflect the weaker defense mechanism of these cultivars in response to the attack by onion thrips.

According to some authors, in resistant plants, besides the presence or absence of certain biochemical compounds or their appearance in response to pest feeding, certain morphological and/or anatomical traits may discourage or hinder a longer and deeper penetration of the leaf tissue by thrips during which insects take up the nutrients they need to survive and develop. The onion thrips population was found to be positively correlated with the thickness of the leaf blade of cotton plants [79]. Contradictory findings have been reported by Raza et al. [80] and Bowman and McCarty [81] who advocated that the thickness of leaf blade and lower epidermis correlated negatively with thrips population in different cotton lines. As well, in the case of onion cultivars, Hanafy et al. [82] reported that the thickness of the epidermis of less infested by onion thrips cv. Red onion) was higher than that on cv. Giza 20 with a higher number of thrips. Abdel-Gawaad et al. [83] suggested that the thick epidermis limited the penetration depth of the mandibles and maxillae during feeding, but several studies have shown that maxillary stylets of several species can extend beyond this distance [84]. According to Chisholm and Lewis [6], the maximum recorded length of maxillary stylet protraction is 27 µm in adult onion thrips, but this length was measured on dead specimens and is probably longer in living specimens, so it seems that mesophyll cells were available for onion thrips in all tested onion cultivars. The thickest epidermis layer was noted for three cultivars, namely Bila, Karmen, and Kristine, the last two of which were found to be the most damaged by onion thrips. Moreover, the largest perimeter and area of epidermal and mesophyll cells) were found in the most damaged (cv. Kristine). On the contrary, the thinnest epidermis was observed in cv. Wenta, which was the most resistant to thrips damage in 2016. Onion thrips may have an affinity for onion cultivars with larger epidermal and mesophyll cells that contain more water and nutrients. The significant and

positive correlation between the damaged leaf area and the size of the mesophyll cell seem to confirm this hypothesis, but more detailed work is required.

As previous studies revealed, there is a correlation between thrips infestation and leaf vascular bundle structure. Hanafy et al. [82] indicated that the number of xylem vessels was higher in the onion blade of cv. Red onion, resistant to onion thrips infestation, in comparison to susceptible cv. Giza. Nevertheless, there is still no firm evidence of whether thrips feed on vascular bundles, and such a possibility is only indicated by the studies of Harrewijn et al. [85]. According to Kucharczyk et al. [86], chrysanthemum thrips, *Thrips nigropilosus* Uzel does not damage vascular bundles while feeding on peppermint leaves. The authors assumed that this was probably associated with the fact that the outer walls of the epidermal cells at the sites of vascular bundles were covered by a thicker cuticle layer than on other cells of leaf epidermis. In our research, we found negative relationships between the number of thrips and all vascular bundle parameters, yet the only correlation between the density of thrips and the mean area of vascular bundles was found to be significant. In turn, the diameter, perimeter, and mean cross-sectional area of vascular bundles are inversely (but not significantly) correlated with the severity of injury caused by thrips feeding. The effect of the size and number of vascular bundles and other cells parameters on thrips feeding requires further and more detailed studies and the results obtained in this study should be treated with great caution, as they concern only one year of research.

During their feeding on host plants, thrips take in carbohydrates, protein, lipids, vitamins, water, inorganic salts, and other nutrients [4]. This may affect plant nutrition and may also lead to compensation, eventually affecting the tolerance [87]. Johari et al. [88] noted that the level of carbohydrates in chili leaves attacked by thrips was reduced by 2.5% in comparison to uninfested leaves. A decrease in the concentration of reducing sugars in banana flowers damaged by banana flower thrips, *Thrips hawaiiensis* Morgan was reported by Yu et al. [89]. In our study, onion thrips affected the nutritional quality of the onion leaves by reducing the content of total soluble sugars and sucrose in all tested cultivars, from 7% to 29.7%, while the contents of reducing sugars varied depending on the cultivar—ranging from an increase of more than 59% to a decrease of 13%. The reductions of total soluble sugars and sucrose in leaves were demonstrated independently of thrips populations and the percentage of damaged leaf area of the onion cultivars tested and a similar decrease was observed for example in resistant cv. Wenta and susceptible cultivars Alibaba and Karmen. In turn, in cultivars like Polanowska, Wenta, and Tęcza, the increase in the contents of reducing sugars was higher than 25% in some years. According to Strauss and Agrawal [90], in many plant species, partial defoliation leads to an increased photosynthetic rate in the remaining plant tissues, suggesting that compensatory photosynthesis is a common physiological response to leaf damage [91]. In conclusion, the different reactions of onion cultivars to injury caused by injuries caused by thrips probably depended on the tolerance of the host plant, but to confirm this mechanism separate tests should be performed under controlled conditions with the same pest pressure.

Damage to plant tissue caused by thrips is often accompanied by ingestion of chloroplast and degradation of chlorophyll and carotenoids [6,92]. In the experiment of Dai et al. [92], chlorophyll a, b and carotenoids were significantly reduced with increased onion thrips damage in leaves of St John's wort (up to 42.6%, 53.0%, and 63.94%, respectively). Thrips attacks on chili leaves reduced the chlorophyll content by 8% [88]. According to Naidu et al. [93], the reduced level of chlorophylls, particularly chlorophyll a which is more directly involved in determining photosynthetic activity [94] may reduce rates of photosynthesis. In our study, the feeding activity of onion thrips caused a decrease in the contents of leaf pigments in all onion cultivars, from about 1% to more than 28%, but the reduction was not always related to the extent of the injuries caused by thrips. The reduction of chlorophyll a was even above 20%, as in the case of cv. Tęcza in 2016. However, despite such a large decrease in chlorophyll a, a high increase in the content of reducing sugars was noticed in the leaves of Tęcza, which might suggest that its tolerance is induced by an increase in the rate of photosynthesis, leading to increased glucose production.

5. Conclusions

A clear conclusion from this study is that thrips damage cannot always be predicted accurately based on the number of thrips, although in many onion cultivars, a higher population of onion thrips promotes more extensive (and more severe) plant injuries caused by thrips. We identified two cultivars Tęcza and Wenta useful for host resistance to thrips abundance and Wenta to thrips feeding damage and we suggest a link between concentrations of carbohydrates and phenolics and antixenotic and/or antibiotic resistance so that breeding for host plant resistance can be advanced more quickly. A positive correlation between the concentrations of the reducing sugars and thrips abundance and conversely negative relationships between the total phenolic content and thrips damage was confirmed from data for both years. However, determining the qualitative and quantitative composition of sugars and phenolics in the leaves of onion cultivar varieties may reveal their role in the resistance of the onion plant to thrips. In turn, the increasing concentrations of total soluble sugars and sucrose significantly decreased thrips damage—but only in 2015. Because of the discrepancy in the results between the two years of this study, the role of total soluble sugars and sucrose for thrips resistance must be interpreted with caution. We suspect that a thinner epidermal layer, a smaller area of epidermal and mesophyll cells, and a smaller diameter of vascular bundles may favor the resistance of onion cultivars to thrips, but further and more detailed studies are required to confirm this hypothesis. Thrips foraging resulted in a decrease in the content of total soluble sugars, sucrose, and plant pigments in the leaves of all onion varieties (except for chlorophyll b in cv. Polanowska in 2016), and their reductions were demonstrated independently of thrips populations and damaged leaf area. Inversely, some cultivars, namely, Polanowska, Tęcza, and Wenta, reacted to the thrips attack with a high increase in reducing sugar content, which was probably due to their tolerance to thrips' feeding.

We suggest that cv. Wenta, which was resistant to abundance, and feeding damage to onion thrips should be recommended for onion growers and breeders, and we believe that both Wenta and Tęcza should be further investigated for the presence of traits that support their lower infestation and/or injury levels.

Supplementary Materials: The following are available online at www.mdpi.com/article/10.3390/agronomy12010147/s1, Figure S1. Rainfall and average daily temperature at the experimental site (Mydlniki, Krakow District, Poland) in the seasons 2015 and 2016. Figure S2. Dynamics population of *Thrips tabaci* (adults and larvae) throughout the whole growing season on onion cultivars in 2015. Figure S3. Mean percentage of damaged leaf area caused by feeding *Thrips tabaci* throughout the whole growing season on onion cultivars in 2015. Figure S4. Dynamics population of *Thrips tabaci* (adults and larvae) throughout the whole growing season on onion cultivars in 2016. Figure S5. Mean percentage of damaged leaf area caused by feeding *Thrips tabaci* throughout the whole growing season on onion cultivars in 2016. Table S1. Significance of sources of variation in one-way ANOVA for a mean number of adult thrips during onion plants colonization, the seasonal mean number of thrips (adults + larvae) throughout the all growing season from tested onion cultivars, and seasonal mean percentage of damaged leaf area caused by feeding thrips in 2015 and 2016, $df = 7$. Table S2. Significance of sources of variation in one-way ANOVA for a mean number of thrips (adults + imago) collected from tested onion cultivars and mean percentage of damaged leaf area caused by feeding thrips in subsequent days of observation in 2015 and 2016, $df = 7$. Table S3. Pearson's correlation between anatomical characteristics of onion leaves and the number of *Thrips tabaci* and percentage of damaged leaf area of onion leaves in 2016 ($n = 8$). Table S4. The contents of sugars and total phenols in damaged by *Thrips tabaci* leaves of the tested onion cultivars in 2015, $df = 7$. Table S5. The contents of sugars and total phenols in damaged by *Thrips tabaci* leaves of the tested onion cultivars in 2016. Table S6. The contents of chlorophyll a and b and the sum of carotenoids in not damaged and damaged by *Thrips tabaci* leaves of the tested onion cultivars in 2015, $df = 7$. Table S7. The contents of chlorophyll a and b and the sum of carotenoids in not damaged and damaged by *Thrips tabaci* leaves of the tested onion cultivars in 2016, $df = 7$. Table S8. Significance of sources of variation in two-way for biochemical parameters of leaves of tested onion cultivars in 2015 and 2016.

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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. Formal agreements for the experiment were obtained from the University of Agriculture in Krakow.

Data Availability Statement: The data presented in this study are openly available in Harvard Dataverse: <https://doi.org/10.7910/DVN/BOROTC>, accessed date 20 November 2021.

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11. Oświadczenia dotyczące udziału kandydata i współautorów



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Oświadczenie o udziale współautora w publikacji

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podpis współautora



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