



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, Tecza 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

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



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Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). 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 Rőth 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 Rőth 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 F_1 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 F_1 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 m^2 (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.

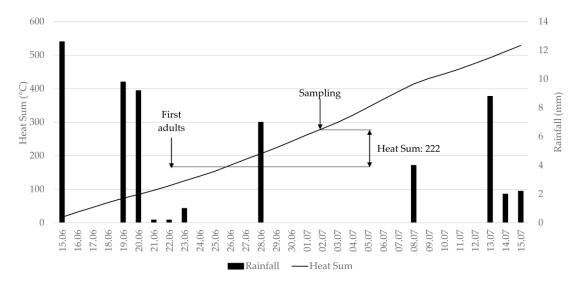


Figure 1. Cumulated effective temperature for the development of *Thrips tabaci* and precipitation recorded in 2015.

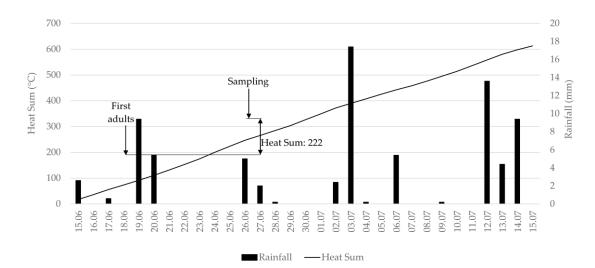


Figure 2. Cumulated effective temperature for the development of Thrips tabaci and precipitation recorded in 2016.

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 \times 4 blocks \times 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 ($d/8^{\circ}$); 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). Oneway 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 F_1 and Bila plants in comparison with the other cultivars except for Karmen, Kristine, and Polanowska. Alibaba and Tecza 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 F_1 and Bila attracted the most adult thrips, while Wenta was the least infested (Figure 3b).

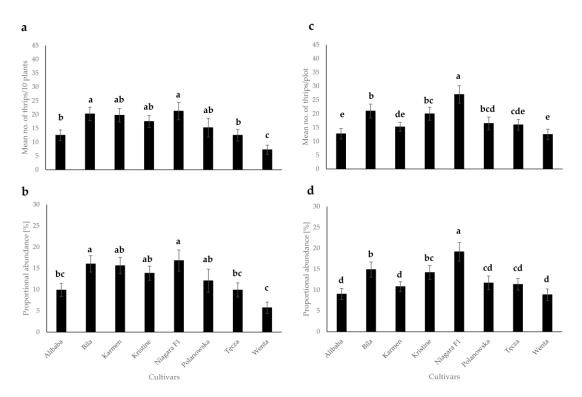


Figure 3. Actual count (mean \pm SE) and proportional abundance of *Thrips tabaci* adults collected (**a**,**b**) directly from plants and (**c**,**d**) with sweep net during onion plant colonization by thrips in 2015. Means with the same letters on each bar are not significantly different (Duncan's 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, Tecza, were the least susceptible to onion thrips infestation (Figure 4a,b).

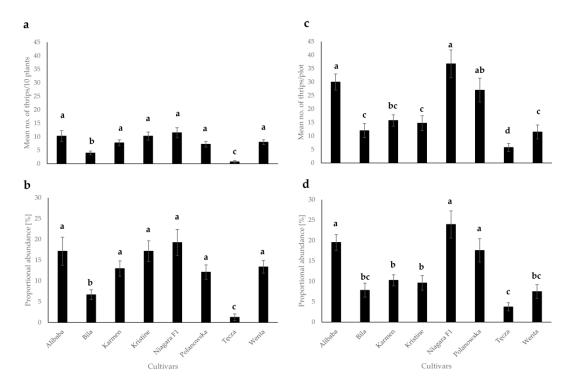


Figure 4. Actual count (mean \pm SE) and proportional abundance of *Thrips tabaci* adults collected (**a**,**b**) directly from plants and (**c**,**d**) with sweep net during onion plant colonization by thrips in 2016. Means with the same letters on each bar are not significantly different (Duncan's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

The mean number of onion thrips specimens collected with a sweep net from Niagara F_1 and Alibaba differed significantly from that collected from the other tested cultivars, except for only Polanowska. Tecza 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 F_1 , Polanowska, and Alibaba attracted the most thrips; Tecza 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 Tecza 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 Tecza differed significantly from Alibaba and Polanowska (Table 1).

Table 1. Colorimetric characteristics of onion leaves in 2015.

		L*a*b* Colour Space	L*C*h Colour Space			
Cultivar	L* 1	a*	b*	C*	h*	
			Mean [±SE]			
Alibaba	45.98 ± 1.04 bc 2	-6.89 ± 0.18 b	$9.88\pm0.88~\mathrm{c}$	$12.07\pm0.82~\mathrm{c}$	-54.75 ± 1.76 c	
Bila	48.64 ± 0.45 a	-7.44 ± 0.24 a	$15.08\pm1.04~\mathrm{a}$	$16.82 \pm 1.03 \text{ a}$	-63.58 ± 0.84 a	
Karmen	$46.61\pm0.39\mathrm{bc}$	-6.41 ± 0.19 b	$10.16\pm0.68~{\rm c}$	$12.02\pm0.68~\mathrm{c}$	-57.56 ± 1.09 b	
Kristine	$44.89\pm0.58~{\rm c}$	-6.88 ± 0.22 b	$10.64\pm0.52~\mathrm{c}$	$12.68\pm0.54~\mathrm{c}$	-57.03 ± 0.84 b	
Niagara F1	$47.68\pm0.73~\mathrm{ab}$	-6.57 ± 0.13 b	$10.54\pm0.12~\mathrm{c}$	$12.42\pm0.16~\mathrm{c}$	-58.07 ± 0.30 k	
Polanowska	$45.29\pm0.98~\mathrm{c}$	$-6.39\pm0.08~\mathrm{b}$	$9.20\pm0.71~\mathrm{c}$	$11.22\pm0.62~{\rm c}$	$-54.89\pm1.08~\mathrm{c}$	
Tęcza	$45.80\pm0.36~\mathrm{c}$	-6.83 ± 0.08 b	$13.36\pm0.67\mathrm{b}$	$15.01\pm0.64\mathrm{b}$	-62.78 ± 0.90 a	
Wenta	$44.79\pm0.36~\mathrm{c}$	$-6.61\pm0.16\mathrm{b}$	$9.54\pm0.56~{ m c}$	$11.62\pm0.55~\mathrm{c}$	$-55.12\pm2.14\mathrm{b}$	
F cultivar	5.740	4.520	13.384	12.183	13.170	
<i>p</i> cultivar	0.000	0.003	0.000	0.000	0.000	
F blocks	4.010	2.380	5.344	4.961	5.230	
<i>p</i> blocks	0.02	0.098	0.006	0.009	0.007	

Note: ¹ L* in L*a*b* colour space is the same as the L*of the L*C*h colour space; ² means 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.

		L*a*b* Colour Space		L*C*h Co	lour Space	
Cultivar	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	$46.05\pm0.23~\mathrm{b}$	-8.98 ± 0.07 b	$17.75\pm0.47~\mathrm{b}$	$19.92\pm0.45\mathrm{b}$	$-63.14\pm0.46~\mathrm{b}$	
Karmen	$46.04\pm0.41~\mathrm{b}$	-8.88 ± 0.22 b	$17.69\pm0.76~\mathrm{b}$	$19.79\pm0.77~\mathrm{b}$	-63.28 ± 0.55 b	
Kristine	49.10 ± 0.80 a	-9.78 ± 0.21 a	$20.51\pm1.18~\mathrm{a}$	22.73 ± 1.16 a	$-64.37\pm0.78~\mathrm{ab}$	
Niagara F ₁	$47.18\pm0.66~\mathrm{b}$	-8.73 ± 0.25 b	$17.90\pm1.22~\mathrm{b}$	$19.93\pm0.55\mathrm{b}$	$-63.95\pm1.02~\mathrm{ab}$	
Polanowska	$46.11\pm0.28\mathrm{b}$	-9.05 ± 0.07 b	$17.45\pm0.39~\mathrm{b}$	$19.66\pm0.36~\mathrm{b}$	$-62.56\pm0.48~\mathrm{b}$	
Tęcza	$46.15\pm0.66~\mathrm{b}$	-8.76 ± 0.20 b	$16.83\pm2.23~\mathrm{b}$	$18.98\pm1.08\mathrm{b}$	$-62.34\pm0.97\mathrm{b}$	
Wenta	46.82 ± 0.35	-8.92 ± 0.15 b	$17.90\pm0.75~\mathrm{b}$	$20.01\pm0.75\mathrm{b}$	$-63.44\pm0.50~\mathrm{b}$	
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	
<i>p</i> blocks	0.526	0.259	0.900	0.849	0.851	

Note: ¹ L* in L*a*b* colour space is the same as the L*of the L*C*h colour space; ² means 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 ($\Delta H^* \ge 1.0$), 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	х	2.15	0.57	0.46	0.66	-0.13	1.85	0.05
Bila	-2.15	х	-1.48	-1.67	-0.83	-2.04	-0.22	-2.06
Karmen	-0.57	1.48	х	-0.13	0.09	-0.53	1.21	-0.51
Kristine	-0.46	1.67	0.13	х	0.30	-0.42	1.39	-0.41
Niagara F ₁	-0.66	1.40	-0.09	0.19	х	-0.62	1.14	-0.60
Polanowska	-0.03	2.04	0.53	0.42	0.62	х	1.76	0.03
Tęcza	-1.85	0.22	-1.21	-1.39	-1.14	-1.76	х	-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	х	0.05	0.47	0.28	-0.38	-0.25	0.11
Karmen	1.06	-0.05	х	0.42	0.22	-0.25	-0.30	0.06
Kristine	0.67	-0.47	-0.42	х	-0.18	-0.69	-0.73	-0.36
Niagara F ₁	0.80	-0.28	-0.22	0.18	х	-0.49	-0.55	-0.18
Polanowska	0.77	0.20	0.25	0.69	0.49	х	-0.06	0.31
Tęcza	1.37	0.25	0.30	0.73	0.55	0.06	х	0.37
Wenta	1.00	-0.11	-0.06	0.36	0.18	-0.31	-0.37	Х

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 Co- — ordinates	Thrips A	dults Collec	ted Directly from	n Plants	Thrips Adults Collected with Sweeping			
	Actual Count		Proportional Abundance		Actual Count		Proportional Abundance	
	r	р	r	р	r	р	r	р
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.

Colour Co ordinates	Thrips A	dults Collec	ted Directly from	n Plants	Thrips Adults Collected with Sweeping			
	Actual Count		Proportional Abundance		Actual Count		Proportional Abundance	
	r	р	r	р	r	р	r	р
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	$-0.174 \mathrm{ns}$	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

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).

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 Tecza and Bila were the least susceptible. The proportional abundance of onion thrips collected directly from Tecza 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 F_1 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 F_1 in 2015, and Alibaba and Niagara F₁ in 2016) were very attractive to *T. tabaci*. In contrast, the resistant cultivars, Wenta in 2015 and Tecza 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 Tecza 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], Birithia 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. Pobożniak [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 F_1 , 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, Tecza 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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