

**Plant morphological and genetic background of resistance to  
onion thrips in white cabbage**

**The Thesis of Doctoral (PhD) Dissertation**

**Fruzsina Róth  
Budapest  
2022**



**Hungarian University of Agricultural and Life Sciences**

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onion thrips in white cabbage**

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## 1. BACKGROUND AND OBJECTIVES OF THE WORK

Damage of onion thrips, *Thrips tabaci* Lindeman (*Thysanoptera: Thripidae*), was first described in the 1980s on white cabbage and has become one of its most significant pests nowadays. It causes the greatest damage in the continental climate and summer cultivation but due to the changing climatic conditions, the damage can occur more and more often in the earliest spring open fields. The only effective protection against thrips damage is the breeding and cultivation of resistant varieties. The biology of onion thrips, the resistance of commercial white cabbage varieties, and the plant characteristics affecting it have been studied in several publications (SHELTON et al. 1988, STONER and SHELTON 1988a, STONER and SHELTON 1988b, FAIL et al. 2008, TRDAN et al. 2008, FAIL et al. 2013, BÁLINT et al. 2013a), however, our knowledge about genetic background of resistance is limited.

One of the ways to breed onion thrips resistant varieties is the indirect method to determine the plant traits that affect resistance following the identification of the resistance sources and the targeted selection for them. Such plant trait may be the thickness of the wax layer on the surface of the leaves (VOORRIPS et al. 2008, TRDAN et al. 2008) or the glucose and fructose content of the leaves (ŽNIDARČIČ et al. 2007, TRDAN et al. 2008). The reflection of the leaves measured in the UV range also shows correlations with the onion thrips resistance of the white cabbage varieties (FAIL et al. 2013).

Another method of supporting breeding process is the identification of chromosomal regions associated with resistance through genetic mapping. With the mapping and application of molecular markers closely linked to these regions, in the framework of MAS (marker-assisted selection), makes possible to monitor resistance independently of environmental factors, even at an early stage of individual development. The only information currently available on the genetic background of resistance in white cabbage can be found in a patent application submitted by Rijk Zwaan seed company (LÖPTIEN 2013). A relatively large region is indicated in the description, on chromosome 2 of the white cabbage. Based on heredity, resistance is characterized as a monogenic, dominant trait (LÖPTIEN 2013), which somewhat contradicts the observation that several morphological and biochemical traits play a role in the development of resistance. If major QTL regions can be accurately identified, molecular

markers can be designed and used in breeding practice to allow direct selection for onion thrips resistance already in the early stages of development.

The aim of our research is to determine the plant traits that can be used indirectly for selection of onion thrips resistant genotypes by examining the variability and genetic background of onion thrips resistance in white cabbage. We also aimed to understand the genetic background of resistance and to identify QTLs suitable for molecular marker development which allows reliable monitoring and following of resistance. Our research aims are summarized in the following points:

1. Comparison of onion thrips resistance of white cabbage varieties and breeding lines belonging to different cultivation groups, better understanding of the mechanism of resistance by examining the immigration and colonization of the pest.
2. Investigation of plant characteristics supposed to affect onion thrips resistance, with special attention to visual stimuli; Determining the wavelengths that most influence the onion thrips host plant selection using sticky color traps.
3. Establishment of a mapping population suitable for the identification of chromosomal regions with major-effect and responsible for quantitative traits, QTLs, which are closely linked to the level of resistance of white cabbage to onion thrips.
4. Collect sufficient accuracy and large amounts of data during phenotyping of the mapping population.
5. Genotyping of the mapping population using SNP markers showing polymorphism between parental lines, then performing QTL analysis comparing phenotypic and genotypic data, identifying QTLs determining the resistance of white cabbage onion thrips and related plant traits; comparison of the results with data available in the scientific literature.
6. Evaluation of the applicability of the results in breeding practice.

## 2. MATERIALS AND METHODS

The location of the four trials in total set for comparison of white cabbage thrips resistance in different growing segments, observation of swarming dynamics, and discovery of the genetic background of the resistance was the Trial Station of Syngenta Kft. in Ócsa. The variability of onion thrips resistance between varieties was examined in the summer fresh market and storage (2011) and early spring (2012 and 2013) segments. Mapping of onion thrips resistance in white cabbage was performed in 2016. The experiments were executed according to the general grower practice. The varieties used in the experiments were ‘Quisor’, ‘Ferro’, ‘Blokator’ and ‘Lennox’ in 2011, ‘Pandion’ and ‘Jetodor’ in 2012 and ‘Pandion’ and ‘Jetma’ in 2013.

To create the mapping population, two elite parent lines were selected which used to produce high-quality and good head-structured storage-type hybrids in practice. The two parental lines are very similar in many morphological traits, but show a large difference in their resistance to onion thrips. The ‘Parent1’ parental line is characterized by a higher level of resistance and the ‘Parent2’ parental line is characterized by a high degree of sensitivity. Families in the mapping population were generated from the F1 plant from parental crossing using the SSD (single seed descent) method, resulting in a total of 210 F5 generation RIL families.

In the variety comparison and swarm dynamics experiments four different colored traps were used - yellow, white, blue and fluorescent yellow - from Plant Protection Institute (Hungarian Scientific Academy, [www.julianki.hu/traps](http://www.julianki.hu/traps)) CSALOMON® trap family to observe the adults flying above the field and to examine the color preference of onion thrips. Color traps were fixed at a height of 60 cm above the ground on a reed stick stabbed in the field. Surface reflection of sticky traps and cabbage leaves in different wavelength were measured using Ocean Optics USB 2000+ portable spectrophotometer, R200-7-UV / VIS reflection probe, PX-2 pulsed Xenon light source (220-750nm) and WS-1 diffuse reflectance standard white. Measurements were performed in the range of 230 to 700 nm at 0.2 nm intervals and the data were processed using SpectraSuite software.

The damage caused by onion thrips in each variety was determined by two metrics, estimating the depth of the damaged leaf layers and the extent of their area compared to the total leaf area. One index is the number of damaged leaf layers (TtDep) and the other one is the value of damage severity (TtSev) on a scale from 0 to 10. We had the possibility to accurately determine the number

of adults and larvae found in the head in the 2012 and 2013 experiments with the help of the Berleese funnels of the Plant Protection Institute. As we do not have information about any other thrips species than onion thrips that occur and cause damage in significant numbers in white cabbage, in the present experiment our hypothesis was that adults and larvae harvested from the heads, as well as thrips individuals counted on sticky grips, also belong to this species, was confirmed by specimens in the randomly selected samples and identified by Dr. Gábor Jenser<sup>†</sup>.

The QTL analysis was based on the 210 F5 families of the mapping population planted in 4 replicates in the 2016 mapping experiment. The following data were collected in the pre-harvest and post-harvest period in the mapping population: plant color, thickness of the wax layer on the leaves surrounding the cabbage head, closure of the head forming leaves, light reflection of the head forming and surrounding leaves, head weight, internal structural filling and the extent of damage caused by onion thrips. Onion thrips damage was determined by peeling 25 leaf layers from a total of 3376 heads harvested in 4 replicates of each family. For each leaf layer, the percentage of leaf area damaged by onion thrips relative to the total leaf area was recorded. For QTL analysis, the mean cumulative value of the four replicates of each family was used, which is derived from the summary of the percentage of damage recorded on 25 leaf layers per head.

‘Parent1’ and ‘Parent2’ parental lines selected and used to create the mapping population was genotyped by using 15,000 SNP (single nucleotide polymorphism) markers in Syngenta France SAS Genotyping Laboratory in 2013. A total of 248 markers showing polymorphism between parental lines were identified, of which 240 markers are codominant and 8 markers are dominantly segregated. The RIL population was genotyped using these 248 polymorphic markers in the F4 generation in 2015. The ‘qtl’ and ‘LinkageMapView’ packages of ‘R’ software (BROMAN and SEN 2009) were used to edit the genetic linkage map and perform QTL analysis. The significance level of LOD values (at  $p < 0.05$  and  $p < 0.01$  levels) was determined by 1000-fold permutation test with Haley Knott regression. Due to the deviation of the distribution of the variables from the normal, we used a ‘cim’ (composite interval mapping) model to map the genome for all traits examined. The significance of the effect of chromosomal regions identified as putative QTLs on the studied phenotypic traits was confirmed by analysis of variance (ANOVA), and in some cases the interactions between them were also demonstrated by ANOVA tests.

The physical positions of the QTLs responsible for the development of onion thrips resistance identified in this experiment, as well as the markers associated with onion thrips resistance in white

cabbage published in a previous study (LÖPTIEN software 2013) was mapped by MapChart software (VOORRIPS 2002) on the TO1000DH *B. oleracea* reference genome (PARKIN et al. 2014).

### 3. RESULTS AND DISCUSSION

The sticky traps deployed during the 2011 summer experiment trapped a large number of onion thrips adults flying over the field during the examined time period. Looking at the summarized catch data of the different colored traps, significantly more adults were found in the fluorescent yellow-colored traps ( $p < 0.001$ ), which is approximately 2.5-fold compared to the yellow and white traps and 4.6-fold higher than the blue traps. Comparing the light reflection spectra of the four different colored traps, it was shown that the fluorescent yellow trap shows the lowest light reflection in the UV range, followed by the blue, yellow and then white traps as the values of the curves increase. The course of the sections representing the UV range of the curves of the four different colors is characterized by a very similar pattern. In the range of visible light, on the other hand, the course of the reflection curves shows much larger differences.

The prominent reflection peak of the fluorescent yellow trap's light reflectance curve, which collects the thrips in the largest number, is in the region between 500 and 530 nm in the visible green color range, and a more moderate peak at 550-560 nm in the yellow range of visible light are found. There was a significant negative ( $p < 0.001$ ) and positive ( $p < 0.001$ ) correlation between the number of thrips caught by traps of different colors and the average reflection on the dorsal side of the leaves forming the head in the 350-360 nm of UV-A range and between 540-570 nm of greenish-yellow regions. Since the high-intensity light reflection in these regions has a repellent (350-360 nm) and attractive (540-570 nm) effect on the onion thrips, it is also assumed that its visual system has at least two photoreceptor systems capable of sensing within these regions.

In the early spring field trials set up in 2012 and 2013, the number of adults and larvae caught in cabbage heads showed varying degrees of correlation with the values of the onion thrips damage inside the heads. In 2012, there was no correlation between the number of adults and the depth of damage/TtDep ( $r = 0.066$  ns) and the severity of damage/TtSev ( $r = 0.400$  ns). In contrast,



the number of larvae showed a significant correlation with TtDep values ( $r = 0.657$  \*\*\*), and the number of larvae was almost significantly correlated with TtSev values ( $r = 0.302$  \*). Analyzing the results of the 2013 experiment, we can discover similar correlations to the first season. There was only a moderate correlation between the number of adults and TtDep ( $r = 0.262$  \*), and there was no significant correlation between adults and TtSev ( $r = 0.208$  ns). In contrast, the number of larvae caught from the heads both showed a significant correlation with TtDep ( $r = 0.531$  \*\*\*) and TtSev ( $r = 0.535$  \*\*\*). The stronger correlation between the number of larvae and the extent of damage compared to the number of adults indicates that the depth and severity of thrips damage in the studied varieties is determined more by the reproductive potential of the immigrating adults in the given varieties and the size of the offspring generations, than amount of initially immigrating specimens.

Thus, in view of the results of the 'Jetodor' variety with a higher level of resistance, the role of antibiosis in the development of resistance should be emphasized, however, the combined effect of several different resistance mechanisms is clearly desirable for the development of the highest level of resistance. Our results confirm that the thrips resistance of white cabbage can be derived from several different sources and influenced by a number of morphological or biochemical plant traits that affect pest development or reproduction. Our experiments in early cabbage trials showed that there may be significant differences in the level of thrips resistance also between the varieties belonging to the early variety group. Based on the two studied years, it can be stated that under favorable environmental conditions, the growing number of thrips populations in the heads can cause significant damage, even in varieties with higher resistance levels.

The F5 RIL population generated to map onion thrips resistance and the affecting plant traits already showed a high degree of phenotypic homogeneity within each family and a high degree of phenotypic variability between the families for numerous plant traits in the 2016 summer experiment. With the extent of onion thrips damage during the growing season of the mapping population reaching the high level typical of the summer period of the continental climate, it was possible to detect a significant difference between the average cumulative thrips damage (Tt) of the population ( $p = 1.24E-43$ ). During the assessment of the damage, some lines showed very good level of resistance, which were characterized by cabbage heads completely free of thrips damage. In contrast, in families more susceptible to onion thrips, the damage was found up to the depth of leaf 25, which often covered more than 50% of the given leaves. The average cumulative value per

family, calculated using damage scored in the heads ranged from 0.13 to 389.56. The mean cumulative value of the family with the most damage was more than 69 times higher than the value found in the sensitive parental line of the population. Among the other plant traits recorded, we also found a high degree of variability between families in the amount of wax layer (WAX) of the cabbage leaves surrounding the head. For the mapping population as a whole, values ranged from 1, where the leaves were not covered at all or only in a very thin layer of wax, to 9, characterizing the individuals with the thickest wax layer in the population. Variability of the values characterizing the density of the internal structure of the head (DEN) between families showed a more moderate picture. The lack of large differences is not surprising in this case, as both parental lines of the mapping population are used to breed storage type white cabbage varieties, in which segment the quality and good filling of the head structure is one of the most important determinants of long-term storability.

However, there were significant differences between the head density of the RIL families ( $p = 4.38E-08$ ). For the three plant traits mentioned, the distribution of the data was different from normal, and different levels of correlation between the traits was detected. There was a moderate negative correlation between the damage caused by onion thrips (Tt) and the wax layer of the leaves surrounding the head (WAX) ( $r = -0.49$  \*\*\*), a much stronger value of 0.97 \*\*\* proves a high degree of positive correlation between onion thrips damage (Tt) and head density (DEN). The head weight (HWEI) of the heads evaluated in the study ranged from 1.3 kg to 3 kg, with a mean value of 2.1 kg. The weight of the heads did not show a significant correlation with any of the examined traits during the correlation analysis, even the correlation coefficient between the head density and the weight of the heads reached only 0.33 \*. The degree of thrips damage did not show a significant correlation with more of the examined plant characteristics, such as the closure of the head forming leaves (PROT), the color of the plants (LCOL) and the calculated average relative reflection of the head forming leaves in the UV-A range of 350-360 nm and visible light in the 540-570 nm range.

The genetic linkage map was generated based on 240 codominant and 8 dominant SNP markers showing polymorphism in the parental lines and RIL population. The markers used in the QTL analysis were able to ensure good coverage of a significant part of the 9 chromosomes of *B. oleracea* genome. An exception to this is chromosome 4, where the distance between the nearest markers on a section was so large that this chromosome was displayed separately by the R/qtl software as the two sections - 4 and 4A during subsequent calculations (Fig. 1). Considering the

proportion of the segregation of the markers for all examined markers, the ‘A’ genotype appeared in 46.2%, the ‘H’ genotype in 11.9%, and the ‘B’ genotype in 41.9%.

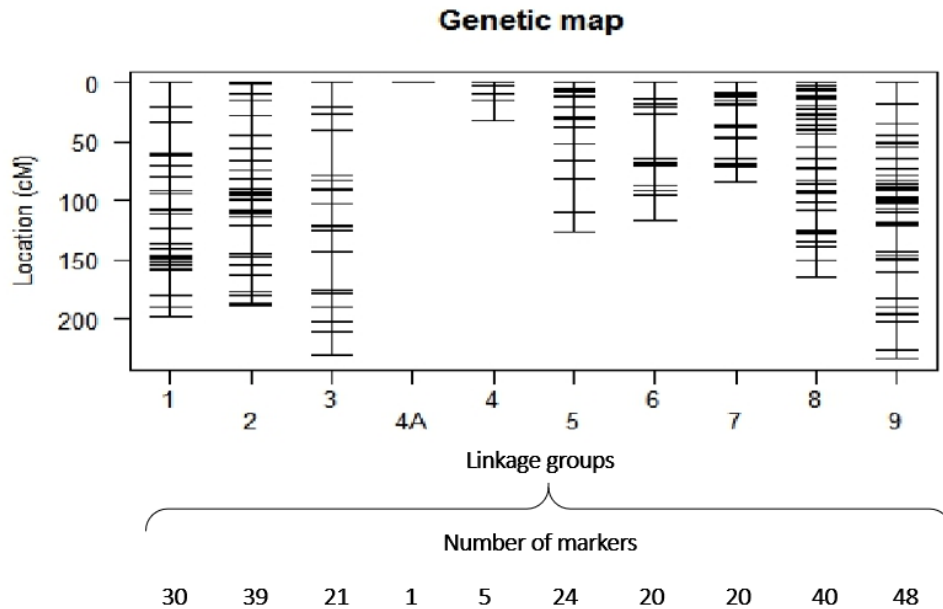


Figure 1.: Genetic linkage map of the white cabbage mapping population according to the 9 chromosomes of *B. oleracea*.

In the mapping population, a total of three loci associated with thrips damage were identified by a complex QTL analysis comparing the damage caused by onion thrips and the data derived from genotyping. The effect of all three identified QTLs was found to be significant, two of them, Ttq1 positioned at 131 cM on Chr2 and Ttq2 mapped to Chr7 at 27.5 cM were characterized as major QTLs and a third Ttq3 mapped at 33 cM to Chr8 as a minor QTL, explains the phenotypic variability of onion thrips resistance in the present mapping population at 28.1%, 21.1%, and 5.2%, respectively (Fig. 2). The closest markers to these QTLs were the SO1546, SO566, and SO1554, respectively. In addition, the smaller interaction identified between Ttq1 and Ttq2 QTLs explains an additional 6.12% of phenotypic variability. Based on a model that includes the three identified QTLs and the interaction between Ttq1 and Ttq2, it can be said that the regions identified here together determine 60.49% of the phenotypic variability of the population. In case of the Ttq1 and Ttq3 QTLs, the allele from the resistant parental line provides a higher level of

resistance, while for *Ttq2*, the reverse is true - the allele of the susceptible parental line is responsible for the higher level of resistance.

In the model containing the three QTLs identified in relation to the thickness of the wax layer, they together contribute 30.9% to the development of the investigated plant trait, of which *Waxq1* (Chr2, 132 cM) and *Waxq3* (Chr7, 34 cM) played a role in the formation of phenotypic variance with 18.01% and 7.58% are more significant than the minor *Waxq2* QTL (Chr3, 225 cM) (Fig. 2), which can be associated with the development of the WAX phenotype in only 5.31%. The markers SO1546 and SO566 closest mapped to the wax layer-associated QTLs we found on the Chr2 and Chr7 linkage groups are identical to the closest markers identified in the regions associated with onion thrips resistance. In addition, the SO409 marker closest to *Waxq2* was identified. For markers SO1546 and SO409, genotypes with a homozygous allele derived from the resistant parental line are characterized by a thicker wax layer on the leaves, while genotypes with a homozygous allele from the sensitive parental line have a more moderate wax-coated phenotype. In the case of the SO566 marker, similar to that observed in onion thrips resistance, a reverse direction of the association was observed, the allele of the susceptible parent was associated with a higher amount of wax, while the allele of the resistant parent was associated with a reduced amount of wax.

The markers mapped in the closest positions of the three QTLs with significant linkage to the density of the heads are the SO1546 marker closest to the 131.5 cM position in the Chr2 linkage group, the *Denq2* QTL to the 28.5 cM position in the Chr7 linkage group, and the SO566 marker, and the *Denq3* QTL marker closest to the 26.1 cM position on the Chr8 linkage group (Fig. 2). These explain 30.91%, 23.42%, and 6.74% of the phenotypic variability in head density in the mapping population, respectively. Considering the two major and one minor QTLs identified, as well as the interaction between *Denq1* and *Denq2* that affected the phenotypic appearance by 7.65%, they together accounted for 68.72% of the trait. Similar to onion thrips resistance and leaf wax mapping results, the SO1546 marker also played a prominent role in the head density as the marker mapped closest to the *Denq1* QTL to the Chr2 linkage group. The allele of the sensitive parental line resulted in a denser, better filling of the cabbage head compared to the allele from the resistant parent, as well as the SO1618 marker identified closest to the *Denq3* QTL. In contrast, the effects of the third allele of the SO566 marker, which was identified as the closest marker to the *Denq2* QTL in the mapping of onion thrips resistance and wax layer, works in the opposite

direction, the resistant parental allele is associated with higher values describing better cabbage head filling.

We were also able to identify QTLs associated with additional plant traits with moderate association to onion thrips resistance - such as head weight (HWEI), leaf color (LCOL), and head-forming leaf closure (PROT) (Fig. 2). Regarding the weight of the heads, a total of five QTLs were identified, one at the 8.7 cM position in the Chr2 linkage group (Hweiq2), explained 12.49% of the phenotypic variability. The four minor QTLs (Hweiq1, Hweiq3, Hweiq4, Hweiq5) were mapped to 157 cM, 0 cM, 7.3 cM, and 125 cM positions in the Chr1, Chr4, Chr7, and Chr9 linkage groups, respectively. Analysis by averaging the values of relative reflectance in the UV-A region between 350 and 360 nm in the dorsal part of the head forming leaves identified a QTL at position 107.7 cM in the Chr1 linkage group, but effect of it was not significant. QTL analysis with LCOL values characterizing the color of the plants identified two major and one minor QTLs, with no significant interaction between them. In the Chr2 linkage group, the Lcolq1 mapped at its 110.5 cM position and the Lcolq3 QTLs mapped to the 9.5 cM position in the Chr7 linkage group are responsible for phenotypic variability in 18.46% and 10.85%, respectively. Their confidence intervals partly overlap with other sections that are also significant for the studied properties. QTL analysis based on the PROT data set characterizing head closure identified a total of four regions in association with this plant trait. Two significant QTLs were mapped on the Chr7 linkage group: the largest of the four, Protq1 with 11.13% effect at the 11.5 cM position, and Protq2 with 5.94% effect at the 34 cM position. The other significant identified regions (Protq3 and Protq4) are located at positions 98.5 cM and 96.6 cM on the Chr8 and Chr9 linkage groups.

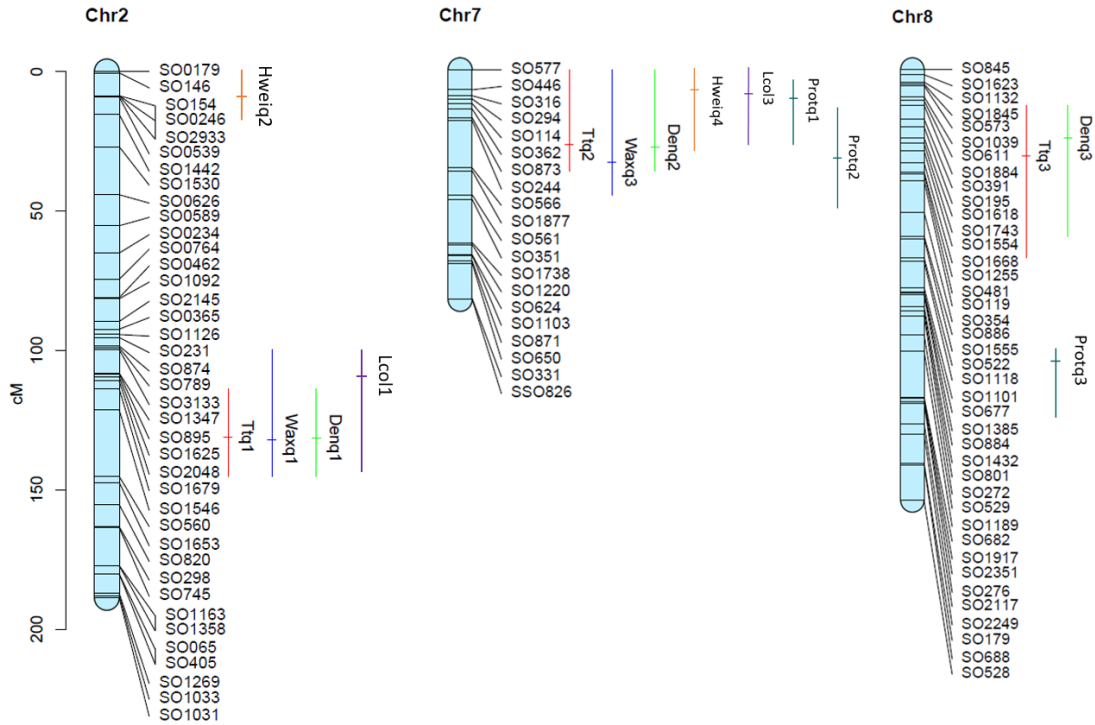


Figure 2.: QTLs identified in the white cabbage mapping population and their confidence intervals.

Short explanation of QTLs: onion thrips resistance (Ttq1, Ttq2 and Ttq3), wax layer of head forming leaves (Waxq1 and Waxq2), head internal density (Denq1, Denq2 and Denq3), head weight (Hweiq2 és Hweiq4), head closure (Protq1, Protq2 and Protq3), and plant color (Lcol1 and Lcol3).

Following the identification of QTLs, high-resolution genetic maps are needed to develop successful practical applications of these chromosomal regions within MAS. The TO1000DH reference genome (PARKIN et al. 2014), which represents 75% of the estimated genome of *B. oleracea*, in addition to the evolution studies, is an excellent tool also for specialists of breeding aiming improvement of any of the large number of cultivated forms belonging this species. From the three chromosomal regions identified in current study and associated with onion thrips resistance, with the SO1546 SNP marker identified closest to the major QTL mapped on Chr2 and the physical position of the SO1679 and SO560 markers determining the QTL confidence interval from both sides can be determined using the TO1000DH reference genome. They could thus be compared with the markers described in the patent under the heading “thrips resistant cabbage”

(LÖPTIEN 2013), including markers BO01146 and BO0200, which were characterized as closest to the resistance gene (Fig. 3).

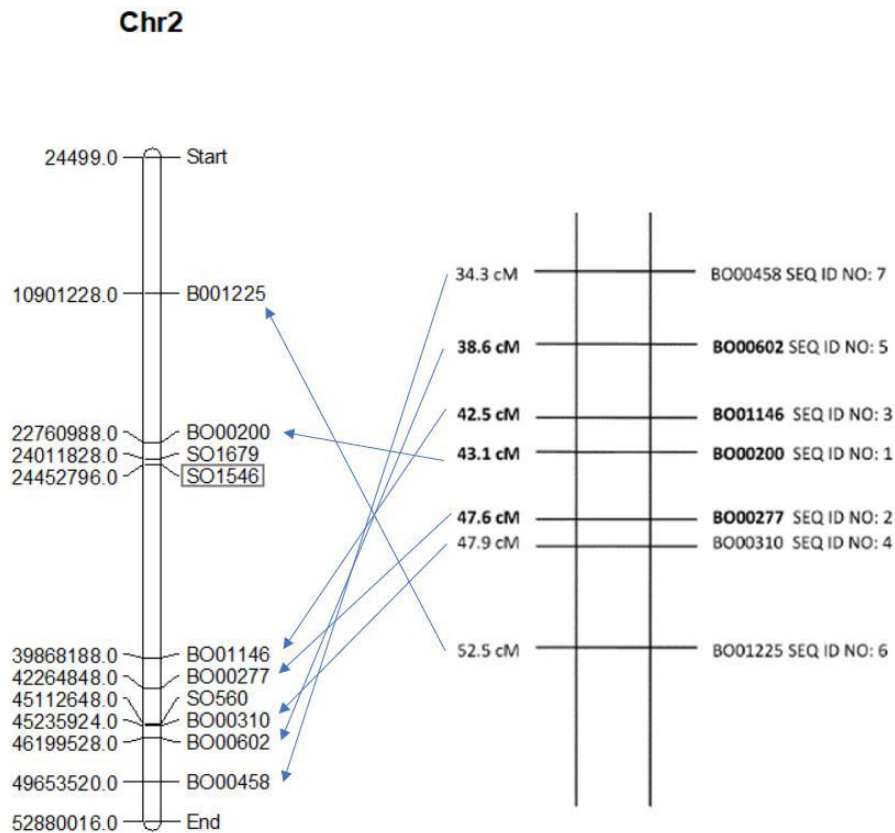


Figure 3.: Physical map of chromosome 2 of white cabbage and genetic linkage map published in the "Thrips resistant cabbage" patent application (LÖPTIEN 2013).

The physical map was prepared based on the TO1000DH *B. oleracea* reference genome (PARKIN et al. 2014), showing the positions of markers mapped closest to the Ttq1 QTL, and the markers of the confidence interval and the positions of the markers reported in the patent application (bp)

The combined physical map shows that the SNP marker SO1546 identified in this research, as associated with onion thrips resistance, is mapped closely or in the same position as the resistance gene described previously. However, a comparison of the physical map created with the genetic map published in the patent shows that in the latter the relatively large distance of 4.5 cM between

the two closest markers may correspond to an even larger chromosome region in reality than expected, as the order of the seven markers on the genetic map shows a significant difference compared to the order of their positions determined by the TO1000DH reference genome (Fig. 3).

#### 4. CONCLUSIONS AND RECOMMENDATIONS

Since visual stimuli have been shown to play a role in the host plants selection of onion thrips, colored sticky traps are excellent tools, not only in plant protection practice, but also in research to understand better the insect's lifestyles and plant resistance mechanisms. These traps can be used to study the response of insects to visual stimuli without modifying the effects to the behavior by additional biochemical or physiological stimuli. The color preference of different *Thysanoptera* species has been investigated in several studies in several cultivated plant species. When comparing the results of these, we may encounter contradictions, the explanation of which may be explained by the presence of additional factors influencing the color preference of insects. It should also be noted that different shades of the same colors may show different efficiencies in different experiments, and subjectively naming the color of the traps used in the experiments does not provide sufficiently accurate information about their physical characteristics. Understanding the color preference of each thrips species is greatly enhanced by understanding the function of their light-sensing system and determining the key wavelengths that characterize their spectral sensing. In the 2011 summer study, we demonstrated a significant effect of trap color also. The low reflectance values of the fluorescent-yellow color traps used in our experiments in the UV range are also likely to play a role in the higher catch rates of these traps. The yellow color range of visible light between 540 and 570 nm is also at least as significant based on the close correlations between the degree of reflection of this region of different colored traps and the number of trapped adults. Based on these results, we hypothesize that onion thrips has at least two different photoreceptors, one in the greenish-yellow 540-570 nm region of visible light and the other in the 350-360 nm region of UV-A.

Varieties belonging to the early growing type are increasingly exposed to onion thrips damage due to climate change and the increasing frequency of rapid warming in the spring, similarly to the summer types, but in most cases very little information is available yet on the level



of resistance of the varieties. Early cabbage experiments set up between 2012 and 2013 confirmed that there may be significant differences in thrips resistance levels between varieties belonging to the early group. Based on the two studied years, it can be said that under favorable environmental conditions, the increasing number of thrips specimens in the heads can cause significant damage, even in varieties with higher resistance level. Tracking the number of individuals colonizing in cabbage heads and size of the offspring generations from their reproduction is great tool for researchers in determining the nature of that interaction between the pest and the plant. In both years, we found that in the more sensitive species, with greater damage, the relative frequency of adults found in the heads broadly followed the swarming curves shown by the sticky traps placed to the field. In the case of resistant and less damaged varieties, this finding did not exist, suggesting that antixenosis plays a role at least in part in the development of onion thrips resistance in cabbage. However, the level of abundance of adults in resistant varieties in the early stages of head formation indicates the presence of additional resistance mechanisms. The much stronger correlation between the number of larvae and the extent of damage compared to the number of adults indicates that the depth and severity of thrips damage in the studied varieties is determined much more by the reproductive potential of the immigrating adults in the given plants, and size of the offspring generations, than the number of initial individuals, so the role of antibiosis in the development of resistance should also be emphasized. Based on the experience of the two years, we can state that the immigration of onion thrips adults and the reproduction of later generations in the head under Hungarian conditions must be expected from April, breeders working with early white cabbage type improvement should pay more attention on onion thrips resistance in the future. Truly effective, stable onion thrips resistance cannot be achieved by indirect selection for antixenotic or antibiotic effects separately, but requires the co-expression of both types of plant resistance.

The identification and mapping of plant sources of resistances is in the focus of many studies due to the appearing and growing plant protection problems worldwide. Most studies are still mainly working on the topic of resistance to various pathogens. There are relatively few publications on the genetic characterization of plant morphological traits, although, as the results described here show, a more detailed understanding of these traits may also help to understand the mechanisms of complex resistance to pests or pathogens. The correlations in the mapping population are also consistent with our conclusions from previous years' experiments that the antixenotic effect of the plant's glossy thick wax layer contributes to the reduction of damage due

to the reduced number of immigrating adults. Our results also showed that the loose structure of the cabbage head further reduces the chances of damage, presumably because the large amount of water typically found between each leaf layer in heads with such a structure can also inhibit the movement, feeding, and reproduction of small insects.

Testing the application of QTLs as widely as possible, demonstrating the efficacy of the markers in different genetic backgrounds, especially for complex plant traits such as resistance to insect pests, is also important for the development of diagnostic markers following genetic mapping. The region described in the patent application by LÖPTIEN (2013) on chromosome 2 of cabbage is presumably the same as or close to the region we also identified on the same chromosome. The description of the patent characterizes thrips resistance as an additive monogenic trait based on the inheritance of the same region (LÖPTIEN 2013), however, this region explained only 28.04% of the phenotypic variability in our mapping population. Based on the two QTLs mapped to chromosomes 7 and 8, thrips resistance in white cabbage is under polygenic regulation and raises the possibility that additional QTLs of thrips resistance may be present in populations with different genetic backgrounds. With our results on onion thrips resistance described here, the work has not been completed, it has just begun. In the future, our goal will be the fine-mapping of the three QTLs associated with thrips resistance, for this purpose the seeds of the next F6 generation of the RIL families are harvested from F5 plants. In the next fine mapping process, we will use more markers and different genetic variants to determine the position of QTLs within the already identified chromosomal regions and to confirm their effect in cabbages of different genetic backgrounds. Because the combined effect of the Ttq1 and Ttq2 QTLs reaches 54% of the population variability even without the third, less potent QTL, it will be worth comparing the variants with the three QTLs to those containing the two highest effect QTLs. If these two regions already provide a sufficient level of resistance, it would greatly facilitate and speed up their practical application. Although well-functioning, tightly linked molecular markers allow the incorporation of a larger number of QTLs into selected elite breeding lines, the time and cost involved will increase significantly as the number of QTLs to be followed increases. The use of diagnostic markers closely linked to QTLs in breeding will allow selection for resistance to onion thrips in the early stages of plant development, even at the seedling stage. By effectively predicting the level of onion thrips resistance in individuals and excluding susceptible individuals at an early stage, we can reduce the size of the experiment to be implanted and focus on the most valuable

genotypes. As a time- and cost-effective process, application of molecular markers developed will greatly help breeders to produce resistant lines and varieties that will also enable growers to defend their crop against onion thrips effectively. The only effective and chemical free solution to the challenges of changing climatic conditions and thus to the rapidly increasing damage of pests in our environment can only be achieved through continuous research and product development, and the knowledge and application of the natural sources of resistance found in plants.

## **5. NEW SCIENTIFIC RESULTS**

1. Our experiments proved that the level of resistance to onion thrips shows a high degree of variability between white cabbage varieties, in the summer-grown segment and also in case of the earliest spring fresh market varieties, where due to the changing climatic conditions we have to expect more significant damage from April.
2. In addition to the importance of antixenotic resistance, the presence of antibiotic resistance effects and the importance in the development of high level resistance were confirmed by monitoring the number of thrips in the heads and the size of the offspring generations in them in different white cabbage varieties.
3. A mapping population of 210 F5 RIL families was created from a cross between onion thrips-resistant and susceptible parental lines, which was found to be feasible for genetic mapping of several traits, including onion thrips resistance in cabbage and its closely related morphological traits.
4. We identified two major (Ttq1 and Ttq2) and one minor (Ttq3) effect QTLs on chromosomes 2, 7 and 8 that show association with onion thrips resistance in white cabbage and including the interactions identified between, together more than 60% of the phenotypic variability observed in the mapping population is explained by them. Thus, we demonstrated that onion thrips resistance in white cabbage is a quantitative trait determined

by several chromosomal regions. In our study, QTLs located on chromosomes 7 and 8 can be identified as novel resistance genes to our current knowledge.

5. Using the mapping population, we identified additional QTLs in white cabbage associated with plant traits in correlation with onion thrips damage. From the QTLs associated with leaf waxiness, one major (Waxq1) on chromosome 2 and two minor (Waxq2 and Waxq3) QTLs were mapped to chromosomes 3 and 7, which together account for more than 30% of the phenotypic variability in the mapping population. From the QTLs associated with head density, the major QTLs identified on chromosomes 2 and 7 (Denq1 and Denq2), together with their interaction and the third minor QTL on chromosome 8 (Denq3), explain more than 68% of the phenotypic variability observed in the mapping population.

## 6. PUBLICATIONS OF THE AUTHOR RELATED TO THE DISSERTATION

Journal articles with Impact factor:

Róth, F., Galli, Z., Tóth, M., Fail, J., Jenser, G. (2016). The hypothesized visual system of *Thrips tabaci* (Lindeman) and *Frankliniella occidentalis* (Pergande) based on different coloured traps' catches. North-Western Journal of Zoology (IF2016 = 0.733), 12(1), 40-49.

Róth, F., Briggs, W. H., van der Ploeg, S., Galli, Z. (2021). Genetic Mapping of QTLs Associated with Resistance against Onion Thrips and Related Morphological Characteristics in White Cabbage. International Journal of Agriculture & Biology (IF2021 = 0.822), DOI: 10.17957/IJAB/15.1876

Publications in peer-reviewed journals (MTA list):

Róth, F., Galli, Z. (2020). Dohánytripsz körkép a zöldségfélék nemesítésének szemszögéből. Kertgazdaság 52(3), 34-48.

Conference abstracts:

Róth, F., Galli, Z., Fail, J., Jenser, G. (2014). *Thrips tabaci* berepülésének és megtelepedésének mértéke különböző káposztafajták esetében. 60. Növényvédelmi Tudományos Napok, szerk. Horvárh, József, Haltrich Attila, Molnár János, Budapest, 29.

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