Note

The relations of broad nematode resistance to quality characteristics as a consequence of marker-assisted selection in potato breeding programs

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Cultivating resistant varieties of potato is the most effective and environmentally sound method of protecting potato crops against pests and diseases. Potato cyst nematodes (PCN) are major nematode pests causing severe constraints in potato production worldwide. There are five pathotypes of *Globodrea rostochiensis* (Ro1–Ro5) and three of *G. pallida* Pa1–Pa3. Cultivation of potato varieties with broad nematode resistance may influence the growth of the wide spectrum of PCN pathotypes, but there is limited availability of such varieties on the market. The use of molecular markers allows for the effective selection of resistant genotypes at early stages of breeding. However, the impact of early selection for nematode resistance on the agronomic value of the final selected clones is a cause of concern for potato breeders. This study investigates the relationships between the presence of the combined resistance genes *H1*, *Gro1-4* and *GpaV_{vrn}*, which confer resistance to the nematodes, and certain agricultural traits. Clones with broad nematode resistance conferred by the genes *H1*, *Gro1-4* and *GpaV_{vrn}* presented yields and tuber morphology traits similar to those of the clones without identified resistance genes.

Key Words: breeding, *Globodera rostochiensis*, *Globodera pallida*, marker-assisted selection, *Solanum tuberosum*.

Introduction

Potato is one of the most important staple foods in the world. Some of the major pests that causes significant damage to potato production and quality worldwide are potato cyst nematodes (PCN): *Globodera rostochiensis* and *G. pallida* (Scurrah *et al.* 2005). Pathotype Ro1 of *G. rostochiensis* is the most widely distributed in Europe. However, annual regional surveys conducted in Poland in the years 2009–2013 showed the presence of a new pathotype of *G. rostochiensis*—Ro5 (Przetakiewicz *et al.* 2017). The spread of *G. pallida* in nematode populations in Europe have been also observed (Minnis *et al.* 2002, Pylypenko *et al.* 2005). The possibility of emergence new pathotypes of *Globodera* spp. on potato fields significantly increases due to easy transfer of potato tubers across European Union countries. PCN pose a real threat to potato production because of their rapid distribution in new territories and long-term survival in soil. One of the most economi-

cally convenient and environmentally sound methods for managing PCN infestations is the use of resistant varieties. Cultivation of potato varieties with broad nematode resistance may influence the growth of the wide spectrum of PCN pathotypes, but there is limited availability of such varieties on the market.

One potential strategy for creating varieties with high levels of durable and broad-spectrum resistance is the combination of resistance loci. Molecular markers linked to the loci of interest can be used in potato breeding for the early selection of promising genotypes. There are diagnostic markers for several genes for nematode resistance (Dalamu *et al.* 2012). Marker 57R linked to the gene *H1* was previously applied and found to be useful in the selection of breeding material resistant to pathotypes Ro1 and Ro4 of *G. rostochiensis* (Milczarek *et al.* 2014, Schultz *et al.* 2012). Marker Gro1-4 linked to the gene *Gro1-4* was found to be useful in the selection of breeding material resistant to pathotypes Ro1 and Ro5 of *G. rostochiensis* (Milczarek *et al.* 2011). The major loci underlying resistance to pathotypes Pa2 and Pa3 of *G. pallida* have been identified in the form of the large-effect QTL *GpaV_{vrn}* (Bryan *et al.* 2002, van der Voort *et al.* 2000), and the potential diagnostic marker HC has been identified (Sattarzadeh *et al.* 2006).

There is a concern, however, that marker assisted selection (MAS) of resistant genotypes may lead to the loss of valuable genotypes if they adversely affect traits such as yields and qualities (Tai and Young 1984). The aim of our research was to assess the relationships between broad resistance to nematodes and some quality traits important in potato breeding.

Materials and Methods

Plant materials

The estimated half-sibling lines were derived from two crosses. Maternal forms were clones 11-VIII-90 and 11-VIII-96 obtained in the same cross (Franzi × 07-VIII-27). They were highly resistant to pathotypes Ro1–5 of *G. rostochiensis* and were donors of the *H1* and *Gro1-4* genes. The variety Innovator was the paternal form. According to The European Cultivated Potato Database (https://www. europotato.org), variety Innovator is resistant to pathotypes Pa2/3 of *G. pallida*. Innovator served as the source of the gene $GpaV_{vrn}$. In total, 107 progeny genotypes from 2 crosses were obtained in a crossing program performed at the Młochów Research Centre (**Table 1**).

Molecular marker assays

All progeny clones were tested for the presence of genes *H1* (marker 57R), *Gro1-4* (marker Gro1-4) and $GpaV_{vrn}$ (marker HC). Total genomic DNA was extracted from leaves using the GenElute Plant Genomic DNA Miniprep Kit (Sigma-Aldrich, St. Louis, MO, USA). PCR amplification of markers 57R, Gro1-4 and HC was performed according to the methods of Finkers-Tomczak *et al.* (2011), Gebhardt *et al.* (2006) and Sattarzadeh *et al.* (2006), respectively.

Test for resistance to nematodes

Clones with the genes conferring resistance to *G. rostochiensis* and *G. pallida* (identified resistance genes: $H1 + GpaV_{vrn}$, $Gro1-4 + GpaV_{vrn}$ and $H1 + Gro1-4 + GpaV_{vrn}$) were evaluated for resistance to pathotypes Ro1–5 of *G. rostochiensis* and Pa2–3 of *G. pallida*. The pathotypes used for inoculation were the Ro1 population "Ecosse" obtained from the collection of Science & Advice for Scottish Agriculture, Scotland (SASA), Ro2, Ro3 and Ro4 local populations (pathotype identity confirmed according to Kort *et al.* 1977), Ro5 population "Harmerz"

obtained from the collection of Institut National de la Recherche Agronomique, France (INRA), Pa3 population "Chavornay" and pathotype Pa2 obtained from the collection of the Federal Research Centre for Cultivated Plants, Germany (JKI).

Resistance screening was conducted with two independent phenotypic tests. The resistance tests were performed according to OEPP/EPPO 2006. Resistance was scored on a 9-grade scale, where score 9 indicates the highest level of resistance. The progeny clone was regarded as resistant when the score was higher than 5.

Screening for agronomic traits

The 2nd and 3rd clonal generations of progeny clones were evaluated in field experiments in 2017 and 2018. The experimental fields were located in a central region of Poland in Młochów. Progeny clones were planted at the end of April and harvested in mid-September. The experiment followed a randomized complete block design. In each of 2 blocks, clones were planted in 7 hill plots. Tubers from all clones were screened for a set of agronomic traits: (a) yield (kg per plant), (b) size on a 9-grade scale (where 9 = the largest), (c) starch content (percentage determined from specific gravity (Zgórska 2001)), (d) regularity of shape on a 9-grade scale (9 = the most regular shape), (e) eye depth on a 9-grade scale (1 = the eye depth > 5 mm; 9 = the eye depth = 0 mm) and (f) defects on a 4-grade scale (1 = high intensity of important defects, such as sprouting, stolons (tubers still have stolons after harvest) or secondary growth; 2 = low intensity of important defects or less important defects, such as cracked skin, fat skin and/or skin with symptoms of diseases (i.e., scab or black specks); 3 = few minor defects; 4 = no defects). Clones with the three identified nematode resistance genes ($H1 + Gro1-4 + GpaV_{vrn}$) were additionally evaluated for cooking quality and crisp color according to Domański (2001), Jakuczun (2001), Flis *et al.* (2017) and Lugt *et al.* (1962).

Statistical analyses

The data from field experiments were analyzed by two-way ANOVA for each trait and, in the case of data for defects of tubers, by the Kruskal-Wallis nonparametric test. After ANOVA, the mean values of groups of clones with zero, one, two or three markers of resistance genes were compared by applying appropriate contrasts. The statistical analyses were performed with the R program (Lenth 2019, R Core Team 2019).

Results

Gene identification

The numbers of clones with the identified resistance genes, confirmed by the amplification of the respective linked markers in the tested progenies, are presented in **Table 2**. Marker 57R was amplified in 53 out of 107 tested genotypes. Marker Gro1-4 was amplified in 58 genotypes.

Table 1. Crosses and progenitors, including their resistance genes and the number of evaluated progeny genotypes

Progeny	Female parent	Resistance genes	Male parent	Resistance genes	Number of progeny clones
I	11-VIII-90	*H1, Gro1-4*	Innovator	$GpaV_{vrn}$	68
II	11-VIII-96				39
				Total	107

Table 2. Number of clones with the identified resistance genes *H1*, *Gro1-4* and *GpaV*$_{vrn}$

Identified resistance genes	11-VIII-90 × Innovator	11-VIII-96 × Innovator	Total
H1	12	1	13
Gro1-4	13	8	21
GpaV$_{vrn}$	4	9	13
H1 + Gro1-4	9	8	17
H1 + GpaV$_{vrn}$	9	4	13
Gro1-4 + GpaV$_{vrn}$	8	2	10
H1 + Gro1-4 + GpaV$_{vrn}$	6	4	10
none	7	3	10

Marker HC was amplified in 46 tested genotypes.

The combinations of genes conferring resistance to *G. rostochiensis* and *G. pallida* (identified genes: *H1 + GpaV*$_{vrn}$; *Gro1-4 + GpaV*$_{vrn}$; *H1 + Gro1-4 + GpaV*$_{vrn}$) were found in 33 clones, which were evaluated for resistance to pathotypes Ro1–5 and Pa2–3. Of the clones tested, 32 were resistant to pathotype Ro1, 25 clones to Ro2, 32 clones to Ro3, 30 clones to Ro4 and 22 clones to Ro5. Regarding resistance to *G. pallida*, out of 33 clones tested, 31 clones were resistant to pathotype Pa2, and all 33 clones were resistant to pathotype Pa3. Resistance to all tested pathotypes was found in 21 tested clones. The results of resistance tests and identified resistance genes for each tested clone are shown in **Supplemental Table 1**.

Agronomic trait assessment

The results from preliminary ANOVA and Kruskal-Wallis tests (**Table 3**) indicated significant differentiation of values of all examined traits among tested clones. It was found that breeding line and year were main factors with effects, significantly affecting the estimated traits. A significant interaction was found for tuber yield, tuber size, regularity of tuber shape and eye depth. The mean values of evaluated traits in the group of breeding lines without genes of resistance and differences (contrasts) between mean values for groups of breeding lines with specified resistance gene(s) and the group of clones without any genes are presented in **Table 4**.

For clones with the identified resistance gene *Gro1-4* and the combination of genes *H1 + Gro1-4*, significantly lower tuber yield, and tuber size were found compared to those in clones without resistance genes. In turn, the regularity of tuber shape in the group *H1 + Gro1-4* was rated higher than in clones without resistance genes. Whereas clones from the group *Gro1-4 + GpaV*$_{vrn}$ had lower regularity of tuber shape than clones without resistance genes. The starch content was significantly elevated in clones with the *H1* gene compared with clones without resistance genes but it was not observed for clones in combination with other resistance genes.

Tubers of clones with identified resistance genes (outside clones with genes *H1 + Gro1-4 + GpaV*$_{vrn}$) stood out, with shallower eyes compared with those of tubers of non-

Table 3. Results of testing the effects of breeding line and year with ANOVA and Kruskal-Wallis tests

Source of variation	Tuber yield (kg/plant)	Starch content (%)	Tuber size	Regularity of tuber shape	Eye depth	Defects of tubers[a]
Breeding line	***	**	***	***	***	*
Year	***	***	***	***	***	nt
Breeding line × Year	**	ns	***	***	***	nt
Mean ± standard deviation	0.8 ± 0.4	14.0 ± 2.1	3.7 ± 1.2	6.1 ± 0.7	6.0 ± 0.7	3.2 ± 1.0

[a] Kruskal-Wallis test; nt—not tested.
***, **, *, ns—significance at p = 0.001, p = 0.01 and p = 0.05, not significant respectively.

Table 4. Mean values of evaluated traits in the group of breeding lines without genes of resistance and estimates of the effect of groups of breeding lines with a specified resistance gene(s)

Presence of resistance genes	Tuber yield (kg/plant)	Starch content	Tuber size	Regularity of tuber shape	Eye depth	Defects of tubers[a]
none	0.8	13.7	3.8	6.0	5.7	3.2
H1	0.8 ns	14.5*	3.9 ns	6.0 ns	6.2***	3.3 ns
Gro1-4	0.7**	14.3 ns	3.5*	6.0 ns	6.2***	3.2 ns
GpaV$_{vrn}$	0.8 ns	13.7 ns	3.7 ns	6.0 ns	6.2***	3.1 ns
H1 + Gro1-4	0.6***	14.1 ns	3.4**	6.2*	6.2***	3.2 ns
H1 + GpaV$_{vrn}$	0.8 ns	14.0 ns	3.7 ns	5.8 ns	6.1***	3.1 ns
Gro1-4 + GpaV$_{vrn}$	0.8 ns	14.0 ns	3.7 ns	5.7**	6.0*	3.1 ns
H1 + Gro1-4 + GpaV$_{vrn}$	0.8 ns	13.8 ns	3.8 ns	5.8 ns	5.9 ns	3.2 ns

***, **, *—the mean value of the group is significantly lower (negative estimate) or higher than the mean value of the group without resistance genes at p = 0.001, p = 0.01, and p = 0.05, respectively.
ns—estimate not significant.
[a] the differences based on the Kruskal-Wallis test.

resistant clones. Regularity of tuber shape and eye depth of clones with genes $H1 + Gro1\text{-}4 + GpaV_{vrn}$ had the level observed in clones without identified resistance genes. All clones with identified resistance genes showed defects of tubers at the level observed in clones without identified resistance genes (**Table 4**).

Clones with combinations of genes $H1 + Gro1\text{-}4 + GpaV_{vrn}$ had cooking types B to BC, making them suitable for salads, purées and fries. These clones were also distinguished by the good taste of their tubers (average rating of 6.5 with a range from 6.2 to 7.4 on a scale of 1–9, where 9 indicates the best taste). The clones evaluated were characterized by non-darkening tubers after boiling (the average rating 10 minutes after boiling was 7.2 and after 24 hours was 6.6), and their suitability for crisps was indicated by an average crisp color score of 7.9 (evaluation of harvested tubers on a 1–9 scale, where 9 represents the lightest crisp color).

Discussion

Cultivation of potato varieties with multiple resistance is the most effective and environmentally safe means to control cyst nematodes in potato fields. One potential strategy for creating varieties with high levels of durable and broad-spectrum nematode resistance is combining resistance loci using selection of molecular markers linked to the loci of interest.

Many PCN resistance loci have already been identified (Dalamu *et al.* 2012). Most of them are QTL regions conferring partial resistance, while some are major genes conferring nearly extreme resistance to one or more pathotypes of *Globodera* spp. Among currently grown varieties, the most frequent gene is *H1*, conferring resistance to pathotypes Ro1 and Ro4 of *G. rostochiensis* (Asano *et al.* 2012, Milczarek *et al.* 2011). In *S. spegazzini*, the gene *Gro1-4* at locus *Gro1* confers resistance to pathotype Ro1 of *G. rostochiensis* (Barone *et al.* 1990, Paal *et al.* 2004). Marker Gro1-4 was also found to be useful in the selection of breeding material resistant to pathotype Ro5 of *G. rostochiensis* (Milczarek *et al.* 2011). Resistance to European Pa2 and Pa3 pathotypes of *G. pallida* is determined by the large-effect QTL $GpaV_{vrn}$ (Bryan *et al.* 2002, van der Voort *et al.* 2000).

The cultivation of potato varieties with multiple nematode resistance genes may effectively provide protection against the wide spectrum of PCN pathotypes. However, there is a concern that the accumulation of resistance genes may result in lower tuber quality. The popular opinion that cyst nematode resistance is associated with deterioration of tuber morphology could be associated with the fact that nematode resistance was historically and particularly important in the Polish breeding of starch potato varieties for which the main selection criterion was starch content and not tuber appearance, as in the case of table varieties. However, in studies on the resistance conferred by the *H1* gene,

it has been shown that this gene does not have negative associations with the quality characteristics of tubers (Milczarek *et al.* 2014). In our previous research, it was also demonstrated that there are no negative relationships between the combined resistance genes *H1*, *Ry-f_sto* and *Rpi-phu1* (conferring resistance to pathotypes Ro1 and 4, potato virus Y and late blight) and tuber quality (Milczarek *et al.* 2017). In the present study, the only adverse relationships between the presence of resistance genes and other traits were found in clones with the *Gro1-4* gene and with the combination of *Gro1-4* and *H1*, which yielded fewer and smaller tubers compared to those of clones without genes for resistance and clones with the combination of *Gro1-4* and $GpaV_{vrn}$ expressed lower regularity of tuber shape. However, the clones with broad nematode resistance conferred by the combined genes *H1*, *Gro1-4* and $GpaV_{vrn}$ expressed yield and tuber morphology traits similar to those of the clones without identified resistance genes. Moreover, clones selected by the markers of these genes were also distinguished by their good tuber taste, non-darkening tuber flesh after cooking and suitability for crisps. Tubers of seedlings with identified *H1* gene were more irregular in shape and had deeper eyes, but this relationship was not observed for successive generations. Clones with identified *H1* gene had similar starch content, but significantly higher starch yield compared with clones without gene *H1* (Milczarek *et al.* 2014). In our next previous work (Milczarek *et al.* 2017), starch content and eye depth were not different among the lines with/without *H1*. In this study, however, significant differences were observed in these traits. It would rather indicate a result of the combination ability of individual parental forms, not a constant tendency associated with the presence of this gene.

Clones with the identified resistance gene *Gro1-4* and the combination of genes *H1 + Gro1-4*, significantly lower tuber yield, and tuber size were found compared to those in clones without resistance genes. It is known that combining ability is an important factor in potato breeding (Gopal 1998); thus, these relationships appear to be related to the influence of the combination of many genes and not the presence of resistance genes.

This study showed that there is no negative relationship between the presence of the combined resistance genes $H1 + Gro1\text{-}4$ and $GpaV_{vrn}$ and the quality of the potatoes. In conclusion, the early selection for combined resistance to nematodes does not adversely impact the agronomic value of final resistant selections.

The results from the presented study strengthened the validity of utilizing the clones with combined resistance genes $H1 + Gro1\text{-}4$ and $GpaV_{vrn}$ in potato breeding programs. The clones developed in this study are valuable breeding materials that provide excellent potential for developing new table potato varieties with high levels of broad nematode resistance.

Author Contribution Statement

Acknowledgments

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