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EFFECTIVENESS OF *PUCCINIA RECONDITA* F. SP. *TRITICI* RESISTANCE GENES AT DIFFERENT PHENOLOGICAL STAGES OF WINTER WHEAT

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Abstract: The resistance of winter wheat varieties to *Puccinia recondite* f. sp. *tritici* was investigated at the Lithuanian Institute of Agriculture during 2001–2003. Effectiveness of resistance genes was investigated at seedling, tillering and adult plant stages. Virulence tests done during the 2000–2003 period showed that the majority of *Lr* genes used in European wheat were not sufficiently efficient. However, testing of cultivars at the first leaf stage revealed that the *Lr37* gene in combination with the other genes was very effective. The experimental cultivars were sown in 2 times: in autumn and spring, without vernalization. The main task of spring-sown nursery was to improve the effectiveness of the experiment and investigate the effect of different *Lr* genes of non-vernalized plants at tillering growth stage. The *Lr37* gene was found to be the most effective at both adult plant stage and tillering growth stage. Disease severity and plant resistance type at tillering stage were stable in all experimental years, which is important for the breeding program. The investigations revealed that the correlations between resistance at seedling and the other two stages were up to r = 0.81 (significant at p = 0.01**). The correlations between leaf rust severity and varietal resistance type at tillering were very high (r = 0.86–0.91**) in the same year. The correlation of leaf rust severity at adult plant stage was strong (r = 0.78**) between 2001 and 2002, but too low for reliable selection of resistant cultivars in the other years. Spring-sown nursery was complementary to collect resistance data in the years unfavourable for leaf rust development.

Key words: winter wheat, leaf rust, resistance genes, growth stages

INTRODUCTION

Leaf rust caused by *Puccinia recondita* f. sp. *tritici* has a worldwide distribution and is the main concern in crophealth programs in many wheat production areas. The development of wheat cultivars carrying diverse rust resistance genes with a broad range of effectiveness and their geographical deployment depending on the pathotype flora provide an effective barrier to control the spread of rust (Macintosh et al. 1995).

West and North European winter wheat cultivars are very variable in terms of their resistance to leaf rust ranging from very susceptible to very resistant. The resistance to leaf rust in this region has moderate importance. On the other hand, when resistance to powdery mildew is one of the mandatory traits of a new cultivar, most of the cultivars, especially the new ones, are resistant or very resistant to this disease (Anonymous 2005). Moderate or low harmfulness of leaf rust is determined by several factors. The first factor is the high intensity of agriculture in Western Europe, which means that winter wheat crop is sprayed with fungicides several times. The second factor is high competition with other leaf diseases, such as tan spot, septoria blotch, powdery mildew and yellow rust.

Leaf rust is more problematic in organic farming system. Winter wheat cultivars intended for organic farming should posses some mandatory traits, such as good competition with weeds, well developed root system and excellent resistance to the main diseases. Special breeding programs to develop varieties for organic farming are expensive, therefore all additional methods which allow to improve effectiveness of testing a large number of breeding lines are highly desirable.

Screening of winter wheat for leaf rust resistance has a few peculiarities. Some resistance genes are effective only at adult plant stage, which means that fast and precise screening at seedling stage is complicated. Another possibility is screening of adult plants in a greenhouse, but it is a costly testing. Screening in a field depends on weather conditions, therefore, precise testing requires installation of special sprayer systems, which have some disadvantages. Preparation and use of inoculum is also rather complicated under field conditions.

Some researchers indicate that *Lr* genes, which are effective mostly at adult plant stage, sometimes are effective at tillering stage too (Park and McIntosh 1994). Winter wheat sown in autumn is sometimes infected with leaf rust, but infection level is too low for resistance evaluation. Winter wheat varieties sown in the spring without vernalization generally do not develop generative shoots. Long vegetative growth period means that in the middle of summer spring-sown wheat plants at tillering stage become exposed to plenty of leaf rust spores from maturing wheat plants and undergo extreme disease pressure. Considering this factor, breeding lines, which are not diseased at tillering stage, should be very resistant at adult plant stage. As a result, the objective of the present study was to analyze the expression of resistance to *Puccinia recondita* f. sp. *tritici* of wheat at the seedling, tillering and adult plant phenological stages.

MATERIALS AND METHODS

Effectiveness of winter wheat leaf rust resistance genes was investigated at the Lithuanian Institute of Agriculture during the period 2000–2003. The first step was to determine the effectiveness of 37*Lr* genes on the background of isogenic lines of the cultivar (cv.) Thatcher. Fifty isolates were tested annually. Effectiveness of *Lr* genes was determined in tests of detached primary leaf segments maintained in plastic box on filter paper moistened with water supplemented with benzimidazole 30 mg/l. Day length was 16-h, night – 8-h, temperature 20±2°C. The scoring was carried out ten days after inoculation. Infection types of 0 to 2 were classified as resistant and those of 3 to 4 as susceptible. Virulence tests were done annually during the experimental period.

Cultivars with known *Lr* genes and used as breeding material were tested at the seedling stage by inoculating with isolates possessing a broad range of virulence genes and were dominant in the tested population. Each cultivar tested was inoculated with 10 isolates in two replications. The tests were done under the same conditions as virulence screening. Cultivars were tested for three years with a new set of isolates each year.

The cultivars tested were sown in the autumn and spring, without vernalization. Autumn sowing was done in the middle of September and spring sowing at the end of May. The main task of the spring-sown nursery was to investigate the possibilities to expand screening of breeding material and to study the effect of different *Lr* genes of non-vernalized plants at tillering growth stage. The soil in a screening plot was clay-loam, with clay content of 24–27%, pH 6.5; percentage of organic matter 2.3–2.5; P_2O_5 150–170; K_2O 180–200 mg/kg of soil. $N_{200}P_{60}K_{60}$ was applied annually. Nitrogen was applied twice: just after resumption of vegetation and at the beginning of stem elongation. Spring-sown nursery was supplied with N_{100} after emergence of seedlings. The genotypes tested were sown after fallow in three replications in different places of the field. The material tested was sown at 3 g per genotype per 1 m row length in 6-row plots. Outside rows were sown with a mixture of cultivars susceptible to leaf rust.

Resistance of breeding material in the field was recorded at late milk stage (BBCH 77) on the flag leaf for autumn-sown plants and at the end of July for spring-sown plants, which were in the state of continuous vegetative growth, when the disease developed up to 100% on susceptible spreaders. Evaluation of leaf rust severity on adult plants was done using the scale: 0, 1, 5, 10, 20, 40, 60, 80, 100%. The severity of leaf rust on the non-vernalized plants was evaluated in the same manner as for adult plants. Resistance reaction to leaf rust was additionally recorded for these plants. The scoring standards were as fallows: 1 – immune (no visible uredia), 2 – very resistant (hypersensitive flecks), 3 – resistant (small uredia with necrosis), 4 – resistant to moderately resistant (small to medium sized uredia surrounded by necrosis or chlorosis), 5 – moderately resistant (medium sized uredia with chlorosis), 6 – moderately resistant to moderately susceptible (medium sized uredia with or without chlorosis), 7 – moderately susceptible (medium to large sized uredia without clear chlorosis), 8 – susceptible (large sized uredia without chlorosis), 9 – very susceptible (large and very abundant uredia without chlorosis) (MacIntosh et al. 1995).

The obtained results were statistically processed using the analysis of linear correlation between disease severities on the tested cultivars at different phenological stages. Means were compared with Duncan's Multiple Range test at the level of significance $p = 0.01$.

RESULTS

Different *Lr* genes widespread in Europe were analyzed. The genes *Lr10*, *13*, *26* and *37* are dominant in European winter wheat cultivars (Winzeler et al. 2000; Park et al. 2001). None of the genes was fairly effective at seedling stage on the background of cv. Thatcher's isogenic lines (Table 1).

This test revealed that *Lr13* was effective against on average 29.0% and *Lr37* against 22.5% of isolates. Genes *Lr13* and *37* are usually expressed at adult plant stage (MacIntosh et al. 1995). These genes should be much more effective in later wheat development stages. Genes *Lr1*, *3*, *10* and *17b* were ineffective and practically had no value for cultivar development. A little more effective was *Lr14a*, but the effect of this gene might have depended mostly on its low occurrence among cultivars. The least infected line possessed *Lr26*, 40% of isolates were virulent in 2000 and only 2% were virulent in 2003. According to these results, cultivars with the same genes tested at the first leaf stage should exhibit similar resistance level.

Table 1. Effectiveness of *Lr* genes on the background of cv. Thatcher's isogenic lines at the first leaf stage

Line	*Lr* gene	Effectiveness of *Lr* genes [%]				
		2000	2001	2002	2003	average
Centenario/6*Thatcher	*Lr1*	26	34	40	30	32.5
Demokrat/6*Thatcher	*Lr3*	28	18	18	12	19.0
Thatcher*6/Exchange	*Lr10*	52	32	62	52	49.5
Thatcher*7/Frontana	*Lr13*	54	28	16	18	29.0
Thatcher*6/Spica	*Lr14a*	56	58	62	62	59.5
Thatcher*6/K. Lucero	*Lr17b*	8	6	50	66	32.5
Thatcher*6/ST-1.25	*Lr26*	60	64	70	98	73.0
Thatcher*8/VPM1	*Lr37*	20	36	20	14	22.5

All cultivars without *Lr* genes were totally susceptible (Table 2). The gene *Lr13*, individually and in combinations, was the most inefficient at seedling stage. Cultivars Mikon (*Lr3*, *13*) and Contra (*Lr13*, *17b*) were susceptible like the cultivars without any *Lr* genes. Other cultivars with *Lr13* were affected by many isolates (53.0–90.0%). Only cv. Pegassos expressed higher resistance, but this effect might have depended on additive effect of *Lr10* (Pretorius and Roelfs 1996). The effect of *Lr13* in combinations was unclear due to the effect of the other genes. The most effective combinations of genes contained *Lr26* or *Lr37*. The exception was cv. Sleipner (*Lr13*, *26*), which was infected by 70% and Renan (*Lr37*) by 90% of isolates. Other cultivars were infected with 0.0 to 30.0% of isolates.

Resistance of winter wheat cultivars at tillering growth stage clearly depended on *Lr* genes. In 2001 the severity of leaf rust varied from 20 to 80% and resistance reaction from 2 to 9 scores. The most diseased cultivars expressed the lowest resistance reaction 8 or 9 scores. The differences between two marginal disease severity values were 4 times. It is noteworthy that the leaves of cultivars with high resistance reaction were affected only by chlorosis or very small uredia. Therefore, self-multiplication of leaf rust on these cultivars was very scarce and actually almost all inoculum for subsequent infections came from susceptible cultivars. The *Lr37* gene was the most effective. Cultivars possessing this gene were infected from 20 to 60% with resistance reaction of 2 scores. The resistance of cultivars with other genes was similar to that of the cultivars without *Lr* genes. Only cvs. Alidos (*Lr14a*) and Tarso (*Lr17b, 26*) exhibited the same resistance as the cultivars with *Lr37*. Resistance of cultivars in 2002 was very similar to that in 2001. Leaf rust severity in 2003 at tillering growth stage

Table 2. Resistance of winter wheat cultivars with known *Lr* genes at different growth stages

Cultivars	*Lr* gene(s)	2001–2003	2001			2002			2003		
		1st leaf	tillering		late milk	tillering		late milk	tillering		late milk
Bussard	–	*100.0 f	**80.0 gh	***9	**46.7 fg	86.7 fg	9	8.3 bc	93.3 hi	9	11.7 e
Konsul	–	100.0 f	60.0 de	7	26.7 de	80.0 fg	8	13.3 cd	46.7 de	8	8.3 de
Kosack	–	100.0 f	66.7 ef	9	66.7 h	80.0 fg	8	26.7 fg	53.3 de	9	3.3 bc
Rector	–	100.0 f	60.0 de	9	20.0 bc	73.3 ef	6	11.7 cd	80.0 fg	9	0.3 a
Zentos	–	100.0 f	60.0 de	7	40.0 ef	80.0 fg	8	33.3 g	60.0 e	8	10.0 de
Lynx	1, 13, 26, 37	0.0 a	26.7 ab	2	0.0 a	46.7 bc	4	5.0 ab	0.0 a	1	0.0 a
Mikon	3, 13	100.0 f	80.0 gh	9	36.7 ef	66.7 de	7	6.7 bc	100.0 i	9	5.0 cd
Pegassos	10, 13	53.0 c	66.7 ef	8	13.3 bc	73.3 ef	8	11.7 cd	66.7 ef	9	1.7 ab
Bandit	10, 37	0.0 a	40.0 bc	2	3.7 ab	60.0 cd	4	6.7 bc	1.7 a	1	1.7 ab
Kris	10, 37	10.0 b	20.0 a	2	2.3 ab	40.0 ab	3	1.0 ab	3.3 ab	3	8.3 de
Siria	10, 13, 26	10.0 b	60.0 de	4	16.7 bc	60.0 cd	4	20.0 de	16.7 bc	4	1.7 ab
Biscay	10, 26, 37	10.0 b	40.0 bc	2	0.0 a	46.7 bc	2	1.7 ab	1.7 a	3	1.7 ab
Kurier	13	75.0 d	86.7 h	9	26.7 de	73.3 ef	8	13.3 cd	20.0 c	5	1.0 ab
Laki	13	75.0 d	73.3 fg	9	23.3 cd	93.3 g	9	11.7 cd	80.0 fg	9	8.3 de
Gawain	13, 14a	90.0 e	60.0 de	9	20.0 bc	73.3 ef	8	20.0 de	60.0 e	9	3.3 bc
Contra	13, 17b	100.0 f	66.7 ef	8	23.3 cd	80.0 fg	8	20.0 de	80.0 fg	9	5.0 cd
Sleipner	13, 26	70.0 d	60.0 de	9	40.0 ef	93.3 g	9	8.3 bc	80.0 fg	9	6.7 de
Brigadier	13, 26, 37	0.0 a	40.0 bc	2	3.3 ab	33.3 a	3	1.7 ab	6.7 ab	3	0.0 a
Alidos	14a	50.0 c	53.3 cd	3	16.7 bc	60.0 cd	3	10 cd	86.7 gh	9	6.7 de
Tarso	17b, 26	0.0 a	40.0 bc	2	13.3 bc	40.0 ab	2	5.3 bc	80.0 fg	9	1.7 ab
Marabu	26	30.0 c	60.0 de	9	36.7 ef	93.3 g	8	2.3 ab	80.0 fg	9	1.0 ab
Previa	26	15.0 b	60.0 de	9	23.3 cd	73.3 ef	7	3.7 ab	86.7 gh	9	3.7 bc
Lone	26, 37	0.0 a	20.0 a	2	6.7 ab	40.0 ab	2	6.7 bc	10.0 bc	3	5.0 cd
Renan	37	90.0 e	60.0 de	2	0.0 a	53.3 bc	3	0.0 a	40.0 d	3	0.0 a

* average percent of virulent isolates
** disease severity, in per cent
*** resistance reaction of cultivar, in scores

differed from that in the two previous years. The cultivars were infected from 1.7 up to 100.0%, but resistance reaction was similar to that in the previous years. Only the cultivar Kurier expressed higher resistance reaction, which increased from 9 scores in 2001 up to 5 scores in 2003. Two cultivars were more susceptible. Reaction of cv. Alidos changed from 3 up to 9 scores and that of cv. Tarso from 2 up to 9 scores. The weather conditions had only inappreciable effect on disease severity and resistance reaction of cultivars at this stage.

Leaf rust severity at adult plant stage was the highest in 2001, lower in 2002 and very low in 2003. The main factor adverse for the development of disease was hot and dry summers in these two years. The marginal values of leaf rust severity were from 0.0 up to 66.7% in 2001, 0.0–33.3% in 2002 and only 0.0–10.0% in 2003. High variation of disease severity was very unfavorable for selection of the most resistant cultivars. The most resistant cultivars in 2001 possessed *Lr37*, gene individually or in combinations. The disease severity ranged from 0.0% (Lynx, Renan) up to 6.7% (Lone). Results of the second year were less clear. The cultivars Marabu, Previa (*Lr26*) and Tarso (*Lr17b, 26*) exhibited the same resistance level as cv. Lynx, Bandit and Lone with *Lr37* in combinations with other gene. Leaf rust severity in 2003 was too low for precise analysis of *Lr* gene effectiveness. However, the effect of unfavorable weather revealed that little effective *Lr* genes can afford some protection.

The investigations revealed the strong correlations (r = 0.68–0.81**) between resistance at seedling and tillering stage in 2001 and 2002 and low in 2003 (Table 3). Weaker correlations (r = 0.43*–0.79**) were found between seedling and adult plants.

Table 3. Correlation between *Lr* genes efficiency and different growth stages in winter wheat cultivars

Year	Growth stage	1	2	3	4	5	6	7	8	9
2001–2003	1st leaf	1.00								
2001 †	tillering	0.81**	1.00							
‡		0.78**	0.86**	1.00						
2002 †		0.68**	0.84**	0.91**	1.00					
‡		0.75**	0.89**	0.92**	0.91**	1.00				
2003 †		0.18	0.23	0.19	0.32	–0.05	1.00			
‡		0.45*	0.57*	0.48*	0.60**	0.33	0.89**	1.00		
2001	late milk	0.63**	0.79**	0.76**	0.71**	0.79**	0.11	0.49*	1.00	
2002		0.79**	0.69**	0.50**	0.41*	0.49*	0.09	0.40*	0.78**	1.00
2003		0.43*	0.31	–0.04	0.25	0.17	0.19	0.32	0.16	0.39

† leaf rust severity,
‡ resistance reaction of wheat cultivars
* significant at p = 0.05,
** significant at p = 0.01

The correlations between leaf rust severity and varietal resistance type at tillering were very high (r = 0.86–0.91**) in the same year. Correlations between different years were very variable (r = –0.05–0.92**), although strong and medium correlations dominated among them. The relationship between disease severity and varietal resistance type between tillering and adult plant stages were very variable (r = 0.09–0.79**) too, when different years were compared.

High variability was due to the dry and hot summers in 2002–2003, when the severity of leaf rust on adult plants markedly decreased compared with 2001, but leaf rust severity and resistance reaction on spring-sown plants were stable. The correlation of leaf rust severity at adult plant stage was strong (r = 0.78**) between 2001 and 2002, but too low for reliable selection of resistant cultivars between other years.

DISCUSSION

Average life of race-specific *Lr* genes of winter wheat is about 3–5 years when cultivars are grown in areas with high rust pressure. In areas with low disease pressure *Lr* resistance genes can be effectively used much longer (Eversmeyer and Kramer 2000). Analysis of virulence of local leaf rust population shows that there were not highly effective *Lr* genes among widely spread genes. However, testing at the first leaf stage revealed effectiveness of *Lr37*. The tested cultivars mainly possessed two or more genes. Isolates with complex virulence were selected, so simple effect of gene pyramiding is not reliable. Probably, there was positive effect of additive gene interactions (Pretorius and Roelfs 1996).

The gene *Lr26* conferred high resistance to some cultivars at adult plant stage in 2002–2003. One of the possible reasons could be that expression of gene *Lr26* can be influenced by genetic background of a cultivar, age of leaf tissue and temperature (Pretorius and Kemp 1990).

Only the *Lr37* gene at tillering and adult plant stages was fairly effective. This gene has been used for about two decades in winter wheat in Western Europe at a frequency of 20–30% (Park et al. 2001), but until now its effectiveness has been very high (Mesterhazy et al. 2000). Our data revealed that at adult plant stage wheat genotypes with *Lr37* were infected by small per cent of *Puccinia recondita* genotypes. Very high efficiency and clear expression of *Lr37* at tillering stage suggests good possibility to screen breeding material for resistance to leaf rust and approximate identification of this resistance gene at this growth stage when frequency of the other effective adult *Lr* genes is very scarce. According to screening of virulence of leaf rust pathogen in North America effective period of *Lr* genes were in close relationship with frequency of cultivars with these genes, time of exploitation of such cultivars and favourability of environmental conditions to leaf rust (Kolmer and Liu 2000; Kolmer and Long 2004). Possibly, the gene *Lr37* will remain effective in Europe until cultivars with this gene have become more frequent. Also, it is noteworthy that climate warming can influence more severe leaf rust epidemics and, as a result, faster adaptation of leaf rust pathogen to this gene.

One of the advantages of screening of breeding material at tillering stage is much longer period available for evaluation of resistance. This period in our investigations was 3–4 weeks at tillering stage, when optimal period suitable for evaluation of adult plants is about 1 week or two weeks in wet and chilly summer. Another advantage was very stable leaf rust severity and cultivar resistance reaction over investigation period compared with the stability of disease severity at the adult plant stage.

Spring-sown nursery was complementary to collect resistance data in the year unfavourable for leaf rust development. Our experimental evidence suggests that studies on leaf rust resistance at tillering stage are a valuable source for screening of winter wheat breeding material for resistance to this disease, especially when the weather conditions are unfavourable for leaf rust development.

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POLISH SUMMARY

EFEKTYWNOŚĆ GENÓW ODPORNOŚCI NA P*UCCINIA RECONDITA* F. SP. *TRITICI* W RÓŻNYCH FAZACH FENOLOGICZNYCH PSZENICY OZIMEJ

W Litewskim Instytucie Rolniczym badano w latach 2001–2003 odporność odmian pszenicy ozimej na rdzę brunatną (*Puccinia recondita* f. sp. *tritici*). Badania efektywności genów odporności prowadzono w fazach siewki, krzewienia oraz na roślinach dorosłych. Testy wirulencji wykonane w trzech latach prowadzenia doświadczeń na 24 odmianach pszenicy ozimej oraz 8 izogenicznych liniach odmiany Thatcher wykazały, że większość genów *Lr* wykorzystywanych w hodowli europejskich odmian nie

była wystarczająco skuteczna. Jednak w toku prowadzenia atestacji odmian w fazie 1. liścia wykazano, że łączne wykorzystanie genu *Lr37* z innymi genami odporności było bardzo efektywne. Gen *Lr37* był najbardziej efektywny zarówno w fazie krzewienia jak i na roślinach dorosłych. Nasilenie choroby i typ odporności w fazie krzewienia były stabilne we wszystkich latach badań, co jest ważne z punktu widzenia programu hodowlanego. Badania wykazały, że współczynniki korelacji pomiędzy odpornością w fazie siewki i dwoma pozostałymi fazami rozwojowymi osiągnęły wartości do r = 0,81 (istotne przy p = 0,01**). Współczynniki korelacji pomiędzy porażeniem roślin w fazie krzewienia a typem odporności odmian w danym roku badań były bardzo wysokie (r = 0,86–0,91**). Korelacja nasilenia porażenia rdzą brunatną w fazie rośliny dorosłej pomiędzy latami 2001 i 2002 była wysoka (r = 78**), ale jednak niewystarczająca, aby można było oprzeć się na niej przy selekcjonowaniu odmian odpornych w innych latach.