

Original Research

Genetic Analysis of Resistance to *Puccinia triticina* Erikss. In *Triticum spelta* L.

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Abstract

Background: Leaf rust caused by *Puccinia triticina* Erikss. is a widely distributed wheat (*Triticum aestivum* L.) disease. Using wild relatives, such as *Triticum spelta* L., as a source of desirable traits represents a good strategy for developing wheat varieties, as *T. spelta* L. has shown tolerance to various types of biotic and abiotic stresses. This study aimed to determine the genetic basis of resistance to leaf rust in the accession *Triticum spelta* 109 (PI 355580). **Methods:** The resistant genotype *T. spelta* 109 was crossed with the bread wheat variety Roelfs F2007, and 135 F₃ families were generated to analyze the genetics of resistance to the MBI/SP leaf rust race. The families were classified into three groups: (i) homozygous-resistant; (ii) homozygous-susceptible; (iii) segregating. A χ^2 test was performed to compare whether the expected and observed segregation ratios fit and to determine the number of genes involved in the resistance of *T. spelta* 109. **Results:** The seedling tests in the F₁ generation showed susceptibility in all plants, indicating that the resistance is conferred by a recessive gene(s). The results of the χ^2 test revealed that the observed segregation ratios of the F₃ families followed the expected values, suggesting that a recessive gene confers the leaf rust resistance present in *T. spelta* 109. According to our results and the reported recessive genes identified among the *T. spelta* accessions, the identified recessive gene in *T. spelta* 109 (PI355580) is different and most likely a novel leaf rust resistance gene. **Conclusions:** The genetic resistance to leaf rust of *T. spelta* 109 (PI 355580) is conferred by a single recessive gene. The importance and usefulness of searching for rust resistance genes from different sources and incorporating them into the genetic base of wheat breeding programs to provide diversity is confirmed.

Keywords: *Puccinia triticina* Erikss.; *Triticum spelta*; genetic resistance; recessive gene

1. Introduction

Leaf rust, caused by the fungus *Puccinia triticina* Erikss. is a widely distributed wheat disease that, when present, can cause significant yield losses [1]. This fungus, due to its biotrophic nature, can produce urediniospores that, disseminated by the wind, infect plants hundreds of kilometers away, often resulting in epidemics on a continental scale [2]. Depending on the severity of the damage to the foliage, the most impactful effect of the disease is reflected in the drastic decrease in the number of grains per head and their weight [2].

Genetic resistance represents the most widely used method to reduce economic and ecological losses caused by leaf rust; therefore, most wheat breeding programs worldwide employ this strategy [3]. Wheat originated in the Middle East and evolved through several natural crosses between related wild species [4]. Subsequently, the use of species related to wheat has made it possible to replicate this process of evolution in different ways [5], becoming, in recent years, one of the most successful ways of sourcing

and taking advantage of the genetic diversity of related and wild species, which provide new genes to the wheat populations presently used in food and agriculture to promote high production, quality, disease resistance, and the necessary safety requirements [6].

Wheat resistance to leaf rust can be classified into two types: (i) race-specific and (ii) partial or slow-developing [7]. Race-specific resistance genes are effective at all stages of plant development. However, race-specific genes expressed at the adult plant stage and poorly expressed in seedlings [7] have also been characterized. Conversely, partial resistance is optimally expressed in adult plants, as seedlings may be susceptible [7]. Resistance to rusts commonly presented by wheat genotypes is known as race-specific; however, the pathogen can overcome such resistance due to continuous evolution toward new physiological races, which is why the constant search for new sources of resistance remains important.

More than 80 leaf rust resistance genes have been catalogued [8], of which almost 50% were derived from wild



or cultivated species closely related to *T. aestivum* L. [9]. Compared to domesticated species, wild relatives retain high levels of genetic diversity [10]; therefore, utilizing the gene pool of their ancestors represents a viable strategy for incorporating desirable traits and developing superior varieties of bread wheat [11].

Triticum spelta L. is a hexaploid species ($2n = 6x = 42$, AABBDD) considered the ancestor of *T. aestivum* [12,13]. *T. spelta* plants are characterized by being tall, with brittle rachis, with long and lax spikes in which the glume is not easily detached, making threshing difficult. Although the presence of these undesirable traits may limit their use as a cultivated species, the production of *T. spelta* plants is preserved due to their tolerance to various types of biotic and abiotic stresses. Meanwhile, *T. spelta* plants have been utilized in the field of genetic improvement as a parent for agronomic traits [14]. There are *T. spelta* accessions in which resistance to diseases has been detected, and upon identification of these resistance genes, the genes were successfully transferred to bread wheat. The resistance genes for leaf rust from *T. spelta* have been catalogued in the Wheat Gene Catalogue [8]: *Lr44* [15], *Lr65* [16], and *Lr71* [17]. A recent study [18], evaluating spelt wheat genotypes for leaf rust resistance, has also identified the presence of *Lr1* and *Lr10*. However, additional resistance factors remain undetected by the currently employed molecular markers. These unidentified factors may include both race-specific resistance genes and non-race-specific adult plant resistance genes [18].

Further resistance genes present in *T. spelta* could be identified and utilized to maintain the diversity of effective genetic resistance in bread wheat germplasm; therefore, additional genetic testing of *T. spelta* is necessary to detect new genes and characterize them according to their genetic action [3].

Due to the constant evolution of the fungus that causes leaf rust towards new races and the need to find new sources of resistance for its control, this study aimed to determine the genetics of a possible new gene toward leaf resistance present in an accession of *T. spelta* (*T. spelta* 109 = PI 355580)

2. Materials and Methods

From a collection of *Triticum spelta* obtained from the germplasm bank of the International Maize and Wheat Improvement Center (CIMMYT), the accession “*T. spelta* 109 (PI 355580)” from Switzerland was selected for its resistance to *Puccinia triticina* Erikss. at the seedling stage against the rust race MBJ/SP according to the nomenclature proposed by Long and Kolmer [19]. Another reason for this selection was that leaf tip necrosis (*Ltn*) was observed at the adult plant stage [20], which is associated with the *Lr34/Ltn1* [21], *Lr46/Ltn2* [22], *Lr67/Ltn3* [23], and *Lr68/Ltn4* genes [24].

“Roelfs F2007” is a spring-growing bread wheat variety developed from the cross Tacupeto F2001/Kukuna, created by CIMMYT and released by the National Institute of Forestry, Agricultural and Livestock Research (INIFAP). Roelfs F2007 is recommended for the autumn–winter production cycles in the northwestern region of Mexico [25]. Moreover, Roelfs F2007 exhibits moderate resistance in the field [25], which is attributed to the presence of adult plant resistance genes *Lr46*, *Lr68*, and *LrB1* (unpublished data). In this study, Roelfs F2007 was susceptible to *Puccinia triticina* Erikss. race MBJ/SP at the seedling stage, so it was used as a susceptible parent to form a segregating population with *T. spelta* 109.

The cross between *T. spelta* 109 and the cultivar Roelfs F2007 was made at the Norman Borlaug Experimental Agricultural Station (CENEB), Ciudad Obregón, Sonora, during the autumn/winter 2018–2019 growing cycle. A total of 20 seeds were obtained from the crosses; of these, 10 were sown, and five F_1 plants were selected. Three of the selected plants were used to advance to the next generation, while the remaining two were retained as reserves. The F_1 seed was sown at El Batán, Mexico, during the 2019 summer cycle to produce the F_2 seed. From each F_1 plant, 50 F_2 seeds were sown at a density of 10 seeds per linear meter in the CENEB field during the 2019–2020 autumn–winter cycle, to obtain 50 individual F_2 plants. During the 2020 summer at El Batán, Mexico, seeds from the F_2 plants were used to generate 50 F_3 families, resulting in a total of 150 families. Of these 150 families, 135 were used for the genetic analysis.

The resistant genotype *T. spelta* 109, the susceptible variety Roelfs F2007, the F_1 generation, and the 135 F_3 families obtained were used for the genetic analysis of resistance. F_2 generation plants were not used to assess resistance; the evaluation of F_3 segregating families was preferred because it represents a more reliable generation, since more than one plant can be observed and counted to determine the type of infection [3].

The evaluation was conducted at the National Laboratory of Rusts and Other Wheat Diseases (LANARET) of National Institute of Forestry, Agricultural and Livestock Research (INIFAP) - Mexico Valley Experimental Field, Coatlinchán, Texcoco, Mexico State 56250, Mexico. The 135 F_3 families, the parents: *T. spelta* 109 and Roelfs F2007, and the F_1 seeds obtained from the crossing of the latter, were sown in plastic trays of 20 cm $\times$ 30 cm $\times$ 6 cm to which a mixture of sterile soil and “peat moss” was added in a 60:40 ratio. In each tray, 10 furrows were marked using a steel plate, and one family per row was sown, with 20–25 seeds placed per family. Five days after planting (DAP), the plants were fertilized using a 20:20:20 formula of nitrogen, phosphorus, and potassium, respectively.

Inoculation was performed 12 DAP using the MBJ/SP leaf rust race of *P. triticina* Erikss. whose avirulence/virulence formula is: *Lr2a*, *2b*, *2c*, *3ka*, *9*, *16*, *18*,

19, 21, 24, 25, 26, 28, 29, 30, 32, 33, 36/1, 3, 3bg, 10, 11, 13, 15, 17, 20, 23, 27+31, 44. A suspension of urediniospores was sprayed in light mineral oil (Soltrol 170, Chevron Phillips Chemical Company, The Woodlands, TX, USA) at a concentration of 5 mg/mL using an atomizer connected to an electric vacuum pump (FE-1500L, Fabricantes Feligneo, Zapopan, Jalisco, Mexico). The plants were left to dry for 15 minutes to allow the excess oil to evaporate, and then were placed in a dew chamber in darkness at 22 °C for 16 hours. Then, the plants were moved to a greenhouse at 24 °C and provided with additional lamp light.

Once the susceptible parent showed visible signs of infection (10 days after inoculation), the infection type of all families was determined using a 0–4 scale [26]. In this scale, “0” depicts immunity, as no uredia or other macroscopic sign of infection is observed; “;” is almost immune because there are no uredia but there are chlorotic or necrotic flecks that indicate hypersensitivity; “1” is very resistant, since small uredia are surrounded by necrosis; “2”, is moderately resistant, since the uredia observed can be small or medium, often surrounded by chlorosis or necrosis and a chlorotic or necrotic border may surround a green island; “X” represents a heterogeneous reaction, i.e., uredia of variable size are randomly distributed on a single leaf. Within the scale, “3” is considered moderately susceptible because there are medium-sized uredia that may be associated with chlorosis; “4” is where large uredia without chlorosis are observed [26]. The scale also included variations or combinations of the infection type, such as “0;”, “;1”, “1+”, or “1+3c”, etc., since it is a relative visual scale.

The families were classified into three groups: (i) homozygous-resistant, with an infection similar to that of the resistant parent; (ii) homozygous-susceptible, with an infection similar to that of the susceptible parent; (iii) segregating, which included plants with an infection similar to those of the two previous groups. Finally, the number of each family in each group was determined, and a χ^2 test was performed using the observed and expected data for a given number of genes. The table value of 5.99, with 2 degrees of freedom ($n-1$), where n is the number of classification groups of F_3 families, and a level of significance $\alpha = 0.05$ [27], was used. Three replicates were conducted, showing the same results in all cases. The mean and variance were not calculated, as a major gene is known to confer the trait.

3. Results and Discussion

Contrasting infection types (ITs) were observed in the parents; *T. spelta* 109 showed “;1”, which is a quasi-immune response characterized by chlorotic or necrotic flecks that indicate hypersensitivity. Roelfs F2007 showed “3” where medium uredia were observed, and some were associated with chlorosis. F_1 also showed the “3” IT (Fig. 1).

Table 1 presents the number of F_3 families registered in each group. Homozygous-resistant families exhibited a

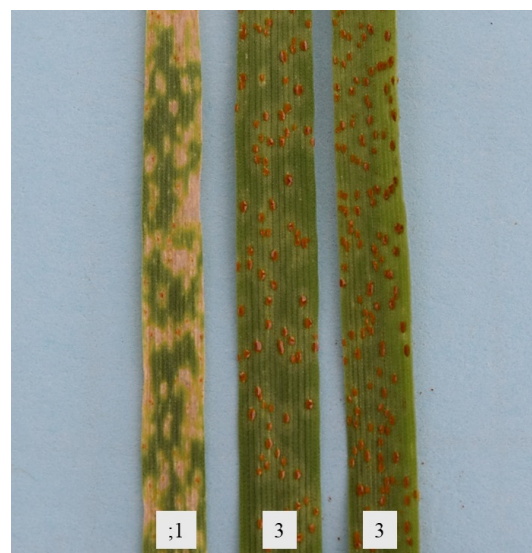


Fig. 1. Parents and F_1 infection types. *T. spelta* 109 (resistant parent) with infection type “;1”, Roelfs F2007 (susceptible parent) with infection type “3”, and F_1 with infection type “3” in seedlings. National Laboratory of Rusts and Other Wheat Diseases (LANARET) of INIFAP-Mexico Valley Experimental Field, Coatlinchán, Texcoco, Mexico State, Mexico, 2024.

Table 1. Number of observed (O) and expected (E) families in F_3 for each family type and chi-square test (χ^2).

Family type	O	E	χ^2_{cal}	χ^2_{tab}
Homozygous-susceptible	34	33.75	0.0019	
Segregating	69	67.5	0.0333	
Homozygous-resistant	32	33.75	0.0907	
Total	135	135	0.1259	5.99

χ^2_{cal} = calculated chi-square ($\chi^2_{cal} = \Sigma(O-E)^2/E$), χ^2_{tab} = tabulated chi-square ($gl = 2$ and $\alpha = 0.05$).

type of infection equal to that of the resistant parent, i.e., IT = 0; (Fig. 2a). Similarly, homozygous-susceptible families showed one type of infection equal to the susceptible parent, IT = 3 (Fig. 2b), and segregating families showed two types of infection: “;1” and “3” (Fig. 2c).

Under the assumption that a major recessive gene promotes resistance, the expected frequencies in F_3 families are 1:2:1, homozygous-resistant, segregating, and homozygous-susceptible, respectively.

When performing the χ^2 test, the results indicated that the observed frequencies followed the expected frequencies, which suggests that a recessive gene confers leaf rust resistance in *T. spelta* 109. Preliminary results (unpublished data) indicate that the gene in *T. spelta* 109 differs from the recessive gene *LrTs276-2*, as indicated by gene-related molecular markers [28]. Since homozygous resistant plants can be easily selected in progeny with a recessive gene, once transferred to bread wheat, the gene that confers

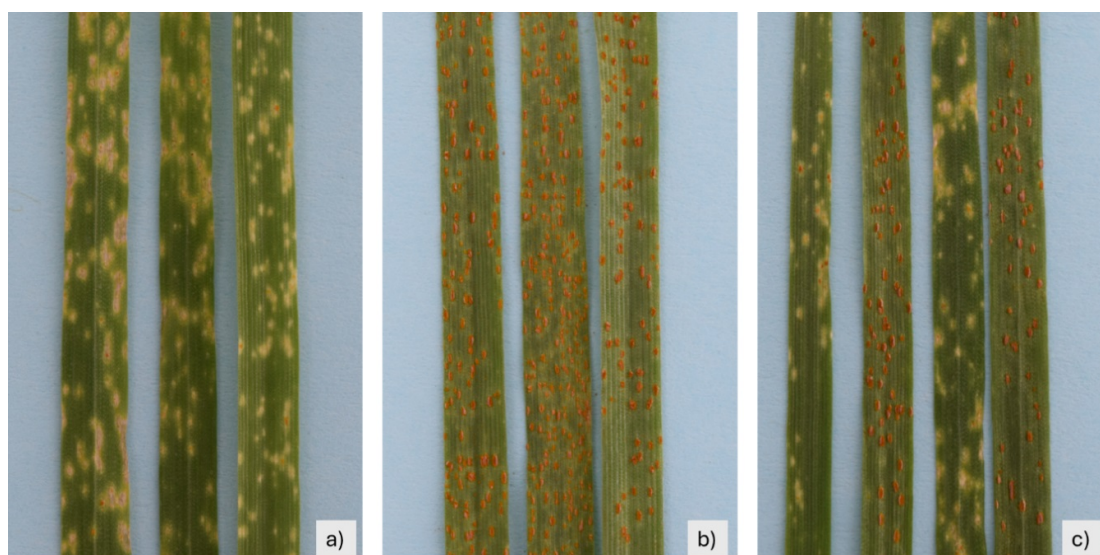


Fig. 2. Infection types observed in the different family groups. (a) Leaves of an F₃ homozygous resistant family at the seedling stage. (b) Leaves of an F₃ susceptible homozygous family at the seedling stage. (c) Leaves of an F₃ segregating family at the seedling stage. National Laboratory of Rusts and Other Wheat Diseases (LANARET) of INIFAP-Mexico Valley Experimental Field, Coatlinchán, Texcoco, Mexico State, Mexico, 2024.

leaf rust resistance in *T. spelta* 109 could be effectively used in wheat breeding programs.

In all the evaluated seedlings from the F₁ generation, an IT of “3” was observed, indicating susceptibility (Fig. 1). This suggests that the resistance is conferred by a recessive gene(s). Other leaf rust resistance genes identified in *T. spelta* accessions, such as *Lr65* and *Lr71*, exhibit a dominant gene action type [28,29]. Conversely, *Lr44* is reported to have partial or recessive genetic action [15]. However, *Lr44* is ineffective against the leaf rust race MBJ/SP used in this study.

Recessive catalogued genes conferring leaf rust resistance are not very common. However, *Lr30* is one of the first reported leaf rust recessive genes [30]. Recently, other recessive genes, such as *LrTs276-2*, have been identified that confer resistance to *Puccinia triticina* Erikss. [28] and the *MIHubel* gene, which confers resistance to *Blumeria graminis* f. sp. *tritici* [31], both have been identified in accessions of *T. spelta*. *Lr83* is also a recessive gene that confers resistance to leaf rust from the *Triticum dicoccoides* species [32].

Among the stripe rust resistance genes cataloged, most are dominant, and a few, such as *Yr3a* [33], *Yr6* [34], *Yr51* [35], and a temporarily designated *YrZ15-1949* [36], are recessive. A similar situation occurs for stem rust catalogued resistance genes, in which only *Sr17* has been reported as recessive [37]. Molecular analysis of the F₃ population is currently being performed to identify a molecular marker linked to the resistance gene temporarily designated *LrT-spelta109* (PI 355580). According to our results and the reported recessive genes identified among the *T. spelta* accessions, the identified recessive gene in *T. spelta* 109 =

PI355580 is different and most likely a novel leaf rust resistance gene which, when combined with other effective and available resistance genes against leaf rust will significantly contribute in developing, through breeding, new and more durable resistant varieties with a broad spectrum against the leaf rust pathogen *P. triticina* Erikss.

Spelt wheat possesses undesirable agronomic traits for modern agricultural systems due to the presence of the *Rht-B1a*, *Rht-D1a*, and *q* alleles, which result in taller plants and tenacious glumes, a vernalization requirement, and photoperiod sensitivity, thereby increasing lodging and hindering mechanical harvesting and processing [38]. Although some of these traits were observed in the germplasm used in this study, future backcrossing to the Roelfs F2007 parent and other bread wheats should be conducted to develop lines that no longer express these undesirable traits.

4. Conclusions

The genetic resistance to rust of the leaf of *T. spelta* 109 (PI 355580) is conferred by a single recessive gene. The importance and usefulness of searching for rust resistance genes from different sources and incorporating them into the genetic base of wheat improvement programs to provide diversity was confirmed.

Availability of Data and Materials

All data reported in this paper will be shared by the corresponding author upon reasonable request.

Author Contributions

JHE, YRVR, IBR, and SD designed the research study. Data collection and analysis: YRVR and JHE. Research project conception and manuscript preparation: YRVR, JHE, IBR, ASV and CMC. All authors contributed to editorial changes in the manuscript. All authors read and approved the final manuscript. All authors have participated sufficiently in the work and agreed to be accountable for all aspects of the work.

Ethics Approval and Consent to Participate

The material used for this study was obtained from CIMMYT (International Maize and Wheat Improvement Center) germplasm bank.

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Conflict of Interest

The authors declare no conflict of interest.

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