Molecular identification of slow rusting resistance \textit{Lr46/Yr29} gene locus in selected triticale (\textit{Triticosecale} Wittmack) cultivars

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Abstract
Recently, leaf rust and yellow rust caused by the fungi \textit{Puccinia triticina} Eriks. and \textit{P. striiformis} Westend f. sp. \textit{tritici} Eriks and Henn are diseases of increasing threat in triticale (\textit{Triticosecale} Wittmack, AABBRR, \(2n = 6x = 42\)) growing areas. The use of genetic resistance is considered the most economical, effective and environmentally friendly method to control the disease and minimize the use of fungicides. Currently, breeding programs mainly relied on race-specific \textit{Lr} and \textit{Yr} genes (\textit{R}), but new races of the rust fungi frequently defeat resistance. There is a small group of genes that causes partial type of resistance (\textit{PR}) that are characterized by a slow epidemic build up despite a high infection type. In wheat slow rusting resistance genes displayed longer latent periods, low infection frequencies, smaller pustule size and less spore production. Slow rusting \textit{Lr46/Yr29} gene, located on chromosome 1B, is being exploited in many wheat breeding programs. So far, there is no information about slow rusting genes in triticale. This paper showed significant differences between the results of identification of wheat molecular markers \textit{Xwmc44} and \textit{csLV46G22} associated with \textit{Lr46/Yr29} in twenty triticale cultivars, which were characterized by high levels of field resistance to leaf and yellow rust. The \textit{csLV46G22res} marker has been identified in the following cultivars: Kasyno, Mamut and Puzon. Belcanto and Kasyno showed the highest resistance levels in three-year (2016–2018), leaf and yellow rust severity tests under post-registration variety testing program (PDO). Leaf tip necrosis, a phenotypic trait associated with \textit{Lr34/Yr18} and \textit{Lr46/Yr29} was observed, among others, to Belcanto and Kasyno, which showed the highest resistance for leaf rust and yellow rust. Kasyno could be considered to have \textit{Lr46/Yr29} and can be used as a source of slow rust resistance in breeding and importantly as a component of gene pyramiding in triticale.

Keywords \textit{csLV46G22} • Molecular markers • \textit{Lr46} • Leaf tip necrosis • Slow rusting • Triticale • \textit{Xwmc44}

Introduction
Triticale (\textit{Triticosecale} Wittmack, \(2n = 6x = 42\), AABBRR genomes) is a man-made amphiploid hybrid produced from the crossing of female parent hexaploid or tetraploid wheat (\textit{Triticum} sp.) and male parent rye (\textit{Secale cereale} L.) (Ammar et al. 2004). It is mostly used in animal feed and biofuel production (Feuillet et al. 2008; McGoverin et al. 2011; Martinek et al. 2008). Triticale, since its commercialization, has shown good resistance to a wide spectrum of pathogens, especially to rusts (Mergoum et al. 2004). As the triticale area harvested has increased, new races of pathogens have adapted to this host (Oettler 2005) and have led to the rapid erosion of effective resistance genes. Leaf rust is one of the most important diseases of wheat (Kolmer 2005), but the pathogen has also been reported on triticale crops (Sodekiewicz and Strzembia 2004). Leaf rust on triticale is caused by pathotypes of the wheat leaf rust pathogen \textit{Puccinia triticina} that have become virulent to triticale genotypes (Sodekiewicz et al. 2008; Mikhailova et al. 2009). Triticale is annually infected by the same spectrum of pathogens as its parents—wheat and rye (Audenaert et al. 2014). To minimize the use of plant protection products, it is necessary to search for and introduce new sources of resistance to varieties. The genetic origin of leaf rust resistance genes in triticale has been studied by several authors. Singh and McIntosh (1990) showed that leaf rust resistance in five triticale varieties was controlled by a single gene designated...
Wilson and Shaner (1989) studied the inheritance of resistance to culture 7434–1 T of *Puccinia recondita* f. sp. *tritici* in four triticales that were selected as potential sources of resistance genes for wheat and described genes for hypersensitive resistance and slow rusting genes in triticale. In Poland, Grzesik and Strzembińska (2003) analyzed leaf rust resistance in three triticle cultivars and showed that the resistance of these cultivars was controlled by the hypersensitive resistance genes described by Wilson and Shaner (1989).

Singh and Saari (1991) identified four resistance genes in three genotypes and two additional genes in triticale in Mexico. Suchliková and Bartoš (1980) analyzed the genetics of resistance to leaf rust in five varieties of triticale in F2 and F3 and postulated five different genes for resistance to leaf rust. Mikhailova et al. (2009) tested 416 triticale from the Vavilov All-Russian Research Institute of Plant Industry and identified 17 leaf rust resistant cultivar. Hanzalová and Bartoš (2011) studied resistance of triticale to wheat leaf rust and analyzed whether specific differences in virulence exist between wheat leaf rust isolates attacking wheat and isolates attacking triticale. They found that leaf rust isolates from triticale were virulent to a higher number of triticale cultivars than isolates collected from wheat.

One of the most effective and environmentally sound methods to control disease is breeding resistant varieties (Dinh et al. 2020). To date, more than 80 genes and alleles of leaf rust resistance (*Lr*) have been identified and described (Mcintosh et al. 2017), but most of this genes are race-specific for hypersensitive resistance (HR). HR genes are very effective in reducing the epidemic build up and easy to introduce in breeding programs because of their monogenic nature, but the resistance provided by these genes can be short-lived as new races of pathogen continue to evolve (Martinez et al. 2001). Kroupin et al. (2019) analyzed the collection of spring triticale accessions for the presence of genes *Lr9, Lr12, Lr19, Lr24, Lr34, Lr28, Lr29* and *Lr47* with the use of molecular markers and isogenic lines carrying target genes. They showed that the gene pool of spring triticale is extremely depleted in leaf rust resistance genes and therefore necessitating work on the introgression of new resistance genes both from the known donor lines of triticale and from bread wheat. It is necessary to search for new sources of resistance or improving intrinsically resistance by gene pyramiding or by use of multilines (McCallum et al. 2007). Another possibility is to incorporate genes that provide partial type of resistance (PR), also known as slow rusting genes or adult plant resistance (APR). PR is a polygenic trait (Parlevliet 1979; Qi et al. 1998) characterized by slow disease progress in the field despite a compatible host reaction (Caldwell 1968). Adult plant resistance (APR) have historically been more durable than race-specific genes (Boyd 2006; Krattinger et al. 2009; Lowe et al. 2011). Slow rusting resistance genes have small to intermediate effects when present alone, so a higher level of resistance is obtained by combining several genes (Singh et al. 2000). In wheat at least seven leaf rust resistance genes are known as slow rusting genes: *Lr34/Yr18* (Singh 1992), *Lr46/Yr29* (Singh et al. 1998), *Lr67/Yr46* (Dyck and Samborski 1979), *Lr68* (Herrera-Foessel et al. 2012), *Lr75* (Singla et al. 2017), *Lr77* (Kolmer et al. 2018a) and *Lr78* (Kolmer et al. 2018b). *Lr34/Yr18* is the leaf rust APR gene with the longest history of resistance, because it has remained effective for almost 100 years (Ellis et al. 2014). *Lr34/Yr18* is the best known slow rusting gene so far. It encodes a modified ATP-binding cassette transporter (Krattinger et al. 2009), and it has been reported to cause an increase in latency period, in percentage of early aborted colonies not associated with cell necrosis and a decrease of colony size (Rubiales and Niks 1995).

*Lr46/Yr29* is the second named gene involved in slow rusting resistance to leaf rust in wheat. *Lr46/Yr29* has provided partial APR to leaf and stripe rust for more than 60 years (Kolmer et al. 2015). It was first described in cultivar Pavon 76 and located on long arm of chromosome 1B (Singh et al. 1998). The effect of *Lr46/Yr29* is similar, but smaller than that of *Lr34/Yr18* in adult plants (Martinez et al. 2001). Lagudah (2011) indicated that *Lr46/Yr29* is more effective in cooler environments and the presence of other *Lr* genes may influence expression of *Lr46/Yr29*. William et al. (2003) found that *Lr46* is linked or pleiotropic to *Yr29* stripe rust resistance gene. Similarly, the close linkage of *Lr34* slow rusting gene to *Yr18* stripe rust resistance gene was identified as well. Wheat genotypes with gene *Lr46/Yr29* were also determined to have stem rust *Sr58* resistance gene (Singh et al. 2013) and powdery mildew (*Pm39*) resistance gene (Lillemo et al. 2008).

Both genes (*Lr34/Yr18* and *Lr46/Yr29*) are associated with a specific phenotypic trait, leaf tip necrosis (LTN) (Singh 1992; Rosewarne et al. 2006). The symptoms could be described as a dying back of the flag leaf from the tip of the leaf (Fig. 1). Leaf tip necrosis is observed to some extent in all wheat varieties containing the leaf rust gene resistance gene *Lr34*. The LTN trait was described by Singh (1992) to be associated with *Lr34/Yr18* locus by investigating a number of crosses between *Lr34/Yr18/LTN* positive lines and *Lr34/

![Fig. 1 Symptoms of leaf tip necrosis on the flag leaf of Kasyno (up) compared with flag leaf of Grenado (down)](image-url)
Yr18/LTN negative lines. It was confirmed by Schnaurbusch et al. (2004) in winter bread wheat cv. "Forno," which has a Lr34 locus associated with LTN. Rosewarne et al. (2006) used field assays to score for both leaf and yellow rust in an Avocet-Yr4 × Attila population that segregates for several slow rusting leaf and yellow rust resistance genes. What is interesting, the offspring population segregated for LTN, which was interpreted as pleiotropic or closely linked to the Lr46/Yr29 locus, and Ln2 gene was suggested designation to this locus (Rosewarne et al. 2006).

So far, there is no information about slow rusting genes in triticale. Wheat cultivars with slow rusting resistance genes displayed longer latent periods, low infection frequencies, smaller pustule size and less spore production. Considering the location of slow rust genes on wheat chromosomes, there is a presumption that it is possible to identify the Lr46/Yr29, Lr68, Lr75 and Lr77 genes (located on 1BL; 7BL; 1BS and 3BL chromosomes, respectively) in the triticale variety. Other slow rusting genes—Lr34/Yr18, Lr67/Yr46 and Lr78 are located on the D genome (7DS, 4DL and 5DS, respectively), which is not present in the triticale genotype. It is entirely possible, that wheat donors of Lr46/Yr29 gene were used in triticale breeding programs. The cross of the hexaploid triticale with and hexaploid bread wheat carrying Lr46 (e.g., Pavon 76), followed by further backcross to triticale could explain its presence in triticale cultivars. It is reported that various wheat-rye translocation lines have been developed to increase genetic variation in wheat and triticale genomes, especially to transfer disease resistance genes and to improve grain yield (Kwiatek and Nawracała 2018). For example, Pavon 1RS near isogenic lines, such as “Pavon 76,” “Pavon 1RS(1),1AL,” “Pavon 1RS(1),1BL” and “Pavon 1RS(1),1DL” developed by Lukaszewski (1993, 2000) are widely used in breeding programs of wheat and triticale (Waines and Ehdaie 2007). The second alternative is the presence of Lr46 in the tetraploid parent used to develop primary triticale (Herrera-Foessel et al. 2012, Li et al. 2020).

Several molecular markers have been developed for Lr46/Yr29 identification. At first, this locus was mapped on the long arm of 1B chromosome using AFLP markers (Wilson and Shaner 1989). Suenaga et al. (2003) revealed that the microsatellite locus Xwmc44 is located 5.6 cm proximal to the putative QTL for Lr46/Yr29. Moreover, it is reported that Lr46/Yr29 locus was mapped distal to Xwmc44, approximately 5–15 cm, and proximal to Xgwm259, approximately 20 cm (https://maswheat.ucdavis.edu/protocols/Lr46). Microsatellite locus Xbarc80 is located 10–11 cm distal to Xgwm259 and is recommended as an alternative distal marker (Lowe et al. 2011). Lagudah et al. (2009, personal communication) developed a cleaved amplified polymorphic sequence (CAPS) csLV46G22 marker which is reported as the closest marker for the Lr46/Yr29 gene, so far (Cobo et al. 2019, Lillemo et al. 2008, Ren et al. 2017). Among all markers available, two closest markers (Xwmc44 and csLV46G22) linked to Lr46/Yr29 were chosen in this study to postulate the presence of Lr46/Yr29 gene in fourteen winter and six spring Polish cultivars of triticale.

### Materials and methods

This study was performed on twenty Polish triticale cultivars derived from Danko Hodowla Roślin Sp. z o.o. breeding company (Table 1). Bread wheat (Triticum aestivum L.) cv. "Pavon F76" (PI 520003) derived from the National Small Grains Collection, the Agriculture Research Station in Aberdeen, was the reference material.

DNA was isolated from the leaves of 10-day-old seedlings with the use of GeneMATRIX Plant and Fungi DNA Purification Kit (EURx Ltd., Poland). DNA concentration and quality was determined using the DeNovix spectrophotometer (DeNovix Inc., USA). The samples were diluted with Tris buffer (EURx Ltd., Poland) to obtain a uniform concentration of 50 ng/μL. To identify the Lr46/Yr29 gene, the molecular markers Xwmc44 and csLV46G22 was used. The sequences of primers are as follows: Xwmc44F 5′-GGT CTT CTG GGC TTT GAT CCT G-3′ and Xwmc44R 5′-GTT GCT GAC CCG TAG TGG-3′. The CAPS marker csLV46G22 tightly linked to Lr46/Yr29 was kindly provided by Dr. Evans Lagudah, CSIRO Plant Industry, Canberra, Australia (personal communication, 2020). The 25 μL polymerase chain reaction (PCR) mixture for Xwmc44 and csLV46G22 consisted of the following: 12.5 μL 2x PCR TaqNovaHs PCR Master Mix (Blirt, Poland), which included 2× concentrated PCR reaction buffer, 4 mm MgCl2; 1.6 mm dNTPs mix (0.4 mm of each dNTP); 1 μL Xwmc44 forward primer; 1 μL Xwmc44 reverse primer (the concentration for each primer was 100 μM); 2 μL DNA template; and 6.5 μL PCR grade water. The PCR was modified on the basis of a standard protocol. The primer annealing temperature of the marker primers was 61 °C for Xwmc44 (Suenaga et al. 2003). The final PCR reaction consisted of initial denaturation at 94 °C for 5 min, followed by 35 cycles (denaturation, 94 °C for 45 s; primer annealing, 61 or 64 °C for 30 s; elongation, 72 °C for 1 min), followed by the final extension for 7 min at 72 °C and storage at 4 °C. The csLV46G22 PCR amplification products were digested with the restriction enzyme BspEI in thermocycler at 37 °C for 1 h (Lagudah, pers. comm. 2020; Ponce-Molina et al. 2018). PCR and digestion was carried out using the Labcycler thermal cyclers (SensoQuest, Germany). The products of amplification were prepared by adding 0.5 Midori Green Direct (Nippon Genetics Europe, Germany) to each tube. The products were separated for one and a half hour using 2% agarose (Sigma-Aldrich, Poland) gel in 1× TBE buffer (BioShop, Canada) at 100 V. To visualize the PCR products, a Molecular Imager Gel Doc™ XR UV system was used with the Biorad Bio Image™ Software (Biorad, USA).
The mean scores of leaf and yellow rust severity were adapted from post-registration variety testing program (PDO) for winter (Drażkiewicz 2019) and spring triticale cultivars (Najewski 2019). This program was performed by the Research Centre for Cultivar Testing (COBORU) and included 3 years (2016–2018) of field scoring of natural infection of *P. triticina* and *P. stiiformis* in fifty localizations in Poland (Zych 2019).

Leaf tip necrosis was scored for twenty triticale accessions in field trial at the Poznan University of Life Sciences. Ten randomly chosen flag leaves were observed and evaluated using positive/negative (LTN+/LTN−) scores (Fig. 1).

### Results and discussion

Most leaf rust resistance genes are race specific (R) and effective during all of the host life cycle, being called seedling genes. Seedling resistance is usually manifested by hypersensitive resistance response (Bolton et al. 2008). Leaf rust resistance conditioned by adult plant genes (APR) can be expressed only at adult plant stage. Some adult plant resistance genes are characterized by conferring partial resistance, which is associated with a slow rusting development instead of a rapid hypersensitive response. Slow rusting genes result in fewer and smaller uredinia and longer latent periods (Lagudah et al. 2009). The partial resistance genes condition longstanding effectiveness. *Lr46* is located on long arm of 1B chromosome and confers a comparable non-hypersensitive type of defense to infection of *P. triticina* as *Lr34* (7DS), but its effect is smaller than that of *Lr34* (Martinez et al. 2001).

In this study, we assumed that *Lr46* gene located on 1B chromosomes could be present in some of triticale cultivars, considering different breeding pathways of primary and secondary triticale. We screened twenty Polish triticale cultivars for *Lr46* using two closest molecular markers and showed that the microsatellite marker *Xwmc44* do not line up with the CAPS marker *csLV46G22* analyses. Microsatellite locus of *Xwmc44* marker is located 5.6 cm proximal to the putative QTL for *Lr46/Yr19* (Suenaga et al. 2003). For comparison, recent maps for *Lr46/Yr19* from Pavon 76 place this locus between *TraesCS1B01G453900* and *csLV46G22* (Lagudah, personal comm.). *Xwmc44* marker was identified in 6 winter cultivars: Dolindo, Fredro, Orinoko, Pizarro, Porto and Trismart (Fig. 2, Tables 1 and 2). Results for *Xwmc44* resistance allele do not coincided with the CAPS marker *csLV46G22* tightly linked to *Lr46/Yr19*. A specific product

### Table 1 Presence of *Lr46/Yr29* gene in tested triticale winter varieties

| No. | Cultivar | Molecular markers | Leaf tip necrosis (LTN) | Leaf rust resistance (scale 1–9)* | Yellow rust resistance (scale 1–9)* |
|-----|----------|-------------------|-------------------------|-----------------------------------|-----------------------------------|
| 1.  | Avocado  | – – – –           | 8.3                     | 8.2                               |
| 2.  | Belcanto | – – + –           | 8.6                     | 8.7                               |
| 3.  | Dolindo  | + – + –           | 8.5                     | 8.0                               |
| 4.  | Fredro   | + – – –           | 7.5                     | 7.5                               |
| 5.  | Kasyno   | – + – +           | 8.5                     | 8.8                               |
| 6.  | Maestozo | – – – –           | 8.3                     | 7.3                               |
| 7.  | Orinoko  | + – – –           | 8.2                     | 7.8                               |
| 8.  | Pizarro  | + – – +           | 8.0                     | 8.4                               |
| 9.  | Porto    | + – – +           | 8.5                     | 8.3                               |
|10.  | Rotondo  | – – – –           | 8.0                     | 6.5                               |
|11.  | Subito   | – – – –           | 8.1                     | 7.5                               |
|12.  | Trapero  | – – – –           | 8.3                     | 8.4                               |
|13.  | Trismart | + – – –           | 6.8                     | 6.8                               |
|14.  | Twingo   | – – – –           | 8.0                     | 8.3                               |

*Scale of the Research Centre for Cultivar Testing (COBORU) in Słupia Wielka (Poland). 9—most resistant; 1—most susceptible. Mean data collected by post-registration variety testing (PDO) in 2016–2018 (Drażkiewicz 2019).*
of csLV46G22 marker was observed in three other triticale cultivars: Kasyno (winter cultivar), Mamut and Puzon (spring cultivars) (Tables 1 and 2). Considering the durability of Lr46 expression, the results of molecular marker analysis were compared with leaf and yellow rust severity in these triticales tested in the field under post-registration variety testing program (PDO 2016–2018; Drążkiewicz 2019, Najewski 2019). Belcanto and Kasyno were the most resistant for infections of both P. titicina and P. stiiformis causing leaf and yellow rust, respectively. The mean score for leaf rust resistance ranged between 6.8 and 8.6 for winter cultivars (Table 1) and 7.5–8.4 for spring cultivars screened in this study (Table 1). Simultaneously, the mean score for yellow rust resistance ranged between 6.5 and 8.8 for winter cultivars (Table 1) and 8.1–8.7 for spring cultivars (Table 2). What is interesting is that the mean scores for leaf and yellow rust resistance for winter cultivars carrying Xwmm44res allele were lower than the mean scores for Xwmc44sus cultivars (Table 1). Considering the second marker, the mean scores for leaf and yellow rust resistance for csLV46G22res cultivars were higher than mean scores for csLV46G22sus cultivars (Tables 1 and 2) with one exception. The scores of yellow rust severity were comparable comparing spring cultivars carrying csLV46G22res and csLV46G22sus (Table 2). The results were also compared with leaf tip necrosis (LTN) analysis. This trait is associated with the Lr34 and Lr46 genes and is a useful phenotypic marker to identify the presence of those genes in wheat lines (Rosewarne et al. 2006). LTN trait was observed only in five winter cultivars (Belcanto, Dolindo, Kasyno, Pizzarro and Porto). The leaf and yellow resistance scores for LTN+ cultivars were higher comparing to LTN− cultivars. Among LTN+ winter cultivars, Dolindo, Pizzaro and Porto

![Electropherogram showing the presence of Xwmc44 marker in the triticale varieties. M, GeneRuler 50 bp DNA ladder (Nippon Genetic Europe, Germany); P, Pavon F76; 1–30, triticale varieties](image)

**Table 2** Presence of Lr46/Yr29 gene in tested triticale spring varieties

| No. | Cultivar | Molecular markers | Leaf tip necrosis (LTN) | Leaf rust resistance (scale 1–9)* | Yellow rust resistance (scale 1–9)* |
|-----|----------|-------------------|-------------------------|----------------------------------|-----------------------------------|
|     |          | Xwmc44 csLV46G22  |                         |                                  |                                   |
| 1.  | Dublet   | – –              | –                       | 7.5                              | 8.5                               |
| 2.  | Mamut    | – +              | –                       | 8.3                              | 8.7                               |
| 3.  | Mazur    | – –              | –                       | 8.2                              | 8.5                               |
| 4.  | Puzon    | – +              | –                       | 8.3                              | 8.1                               |
| 5.  | Santos   | – –              | –                       | 8.4                              | 8.5                               |
| 6.  | Sopot    | – –              | –                       | 8.0                              | 8.4                               |
|     | **Total resistance (scale 1–9)* mean** |                |                         | **8.1**                          | **8.5**                           |
|     | **Resistance (scale 1–9)* mean for Xwmc44res** |              |                         | n/a                              | n/a                               |
|     | **Resistance (scale 1–9)* mean for Xwmc44sus** |              |                         | 8.1                              | 8.5                               |
|     | **Resistance (scale 1–9)* mean for csLV46G22res** |             |                         | 8.3                              | 8.5                               |
|     | **Resistance (scale 1–9)* mean for csLV46G22sus** |            |                         | 8.0                              | 8.5                               |
|     | **Resistance (scale 1–9)* mean for LTN+** |            |                         | n/a                              | n/a                               |
|     | **Resistance (scale 1–9)* mean for LTN−**      |            |                         | 8.1                              | 8.5                               |

*a*Scale of the Research Centre for Cultivar Testing (COBORU) in Słupia Wielka (Poland). 9, most resistant; 1, most susceptible. Mean data collected by post-registration variety testing (PDO) in 2016–2018 (Najewski 2019)
carried \textit{Xwmc44res} allele, when Kasyno was identified to have \textit{csLV46G22res} allele.

Considering the results of molecular markers compared with 3 years of leaf and yellow rust severity tests and LTN trait scoring, it could be assumed that triticale cv. Kasyno could be considered to have \textit{Lr46/Yr29} gene. What is more basing on high levels of leaf and yellow rust resistance and the presence of LTN trait is that triticale cv. Belcanto could be suspected to have \textit{Lr34/Yr18} gene. However, this requires additional molecular marker investigation, which falls outside the scope of this study. In addition, these cultivars may serve as the starting material for pyramiding slow rusting resistance genes in triticale genotypes.

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Authors’ contributions MK initiated the project. RS made the experiments and analyses, wrote the first draft and incorporated all inputs from co-authors. MK, AT and JN revised the draft and made suggestions for improving the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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