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Response of an International Triticale Collection to *Puccinia triticina* and *Puccinia recondita* sensu stricto and Assessment of Temperature Sensitivity in Leaf Rust Isolates

N. Yekelo, L. Rothmann, C.M. Bender, Z.A. Pretorius and W.H.P. Boshoff*

Department of Plant Sciences, University of the Free State, P.O. Box 339, Bloemfontein 9300, South Africa

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Triticale is derived from a cross between wheat and rye and the leaf rust pathogen of wheat, *Puccinia triticina* (*Pt*), and that of rye, *P. recondita* sensu stricto (*Pr*), can potentially cause disease in this crop. Recent studies showed that wheat rust fungi could adapt to warmer temperatures. In this paper, we report on the comparative virulence of three *Pt* races and one *Pr* isolate (all were collected in South Africa) on triticale as well as their *in vitro* response to temperature. Seedling infection types (SITs) of 169 triticale entries to *Pt* races 3SA144 (North American code SDDN), 3SA145 (CCPS) and 3SA248 (CFPS) and *Pr* isolate UVPr2 revealed that 3SA144 is the most virulent with 106 triticale entries found susceptible to this race. The three *Pt* races were avirulent to the four rye cultivars included as controls. UVPr2 was avirulent on all the triticale entries and 49 entries were considered resistant to the *Pt* races tested. Freshly harvested urediniospores of the above isolates were tested at constant temperature regimes of 10 °C, 22.5 °C and 35 °C to study germination characteristics. Mean urediniospore germination percentages as determined for 3SA144 (61.3%) and UVPr2 (62.6%) were significantly lower when compared to 3SA145 (83.7%) and 3SA248 (84.9%). Race 3SA144 was most sensitive to the higher temperature regime of 35 °C (5.2% germination). Among the investigated races, 3SA144 showed significantly lower mean germ tube elongation rates at all three incubation temperatures. This is the first report of differences in temperature adaptation between *Pt* races from SA.

Keywords: *Puccinia triticina*, *Puccinia recondita* sensu stricto, leaf rust, temperature sensitivity

Introduction

Rust pathogens are known for their ability to adapt and evolve posing recurring threats to modern agriculture in a spatially and temporally changing environment (Mboup et al. 2012; Helfer 2014; Hussain et al. 2017; Pretorius et al. 2017). Rust epidemics resulting from frequent virulence changes, long distance dispersal as well as their adaptation to higher temperatures confirms the importance of cereal rust pathogens (Milus et al. 2006; Milus et al. 2009; Huerta-Espino et al. 2011; Meyer et al. 2017; Kolmer and Hughes 2018).

*Corresponding author, E-mail: boshoffwhp@ufs.ac.za; Phone: +27 051 401 2466

Wheat (*Triticum aestivum* L.) leaf rust caused by the fungal pathogen *Puccinia triticina* Erikss. (*Pt*) (Anikster et al. 1997) can cause significant yield losses on cultivated wheat. *Pt* has also been reported on several other host plants including triticale (× *Triticosecale* Wittm.) (Bolton et al. 2008; Chai et al. 2016). Triticale is a hybrid between rye and wheat and consequently the same spectrum of fungal diseases occurring on the parent crops can impede optimal triticale production (Audenaert et al. 2014). Therefore, not only *Pt*, but also leaf rust of rye, caused by *P. recondita* Roberge ex Desm. sensu stricto (*Pr*) (Liu et al. 2013), could be important diseases in this crop.

Increased incidence of *Pt* in spring wheat fields in the Southern Cape, South Africa (SA), as well as the identification of four new races in this region, between 2012 to 2016, have re-emphasised the importance of leaf rust (Boshoff et al. 2018). Air temperature and free moisture on plant surfaces are considered key factors for rust infection (Stubbs et al. 1986; De Vallavieille-Pope et al. 1995). Apart from a report of leaf rust on wild rye (Pretorius et al. 2015) limited information exists for the occurrence of *Pr* in SA. In a recent study, *Pr* isolates UVPr1 and UVPr2 collected from rye at diverse localities in SA were found identical in virulence on rye cultivars planted as forage crops (Boshoff et al. 2019).

In 2005, *Pt* race 3SA144 was collected from triticale in SA and was reportedly more virulent towards triticale and more avirulent towards wheat when compared with other SA wheat leaf rust races (Pretorius and Bender 2010). Despite the initial characterisation of 3SA144, its pathogenicity on diverse triticale germplasm has never been determined. It would also be useful to establish whether the newly identified wheat leaf rust race 3SA248 which attacks *Lr26*, shows increased virulence towards triticale when compared to the older but genetically related race 3SA145 (Terefe et al. 2011; Visser et al. 2011; Boshoff et al. 2018).

The aim of this study was to determine the comparative virulence of the *Pt* races 3SA144, 3SA145, and 3SA248 as well as the *Pr* isolate UVPr2 on a collection of 169 triticale germplasm stocks originating from 17 countries. The influence of temperature on urediniospore germination and germ tube development was also determined using the same rust isolates.

Materials and Methods

Seedling infection types

To obtain fresh and pure cultures the respective *Pt* and *Pr* races were increased on host selective entries in a greenhouse. These hosts included the wheat cultivar PAN3515 (3SA248), a wheat line with *Lr3ka* (3SA145), the triticale cultivar Tobie (3SA144) and the rye cultivar Sorom (UVPr2). Seedlings were established by planting 250 kernels of each entry in five 10 cm diameter pots using a Mikskaar® professional potting substrate MPS2. At coleoptile emergence, four days after planting, seedlings were drenched with 99% maleic hydrazide Reagent Plus® [(Sigma-Aldrich (0.3 g/L water, 50 ml per 10 cm pot)]. Seedlings were fertilized with Multifeed-Classic water-soluble fertilizer [Effekto®,

NPK Analysis 19:8:16 (43)] applied twice a week at a concentration of 2 g/L water. Eight days after planting, seedlings were inoculated using urediniospores of the respective rust isolates retrieved from the University of the Free State's long-term rust culture collection kept at –80 °C. Urediniospores were heat shocked at 46 °C for 6 min in a water bath before being suspended in Soltrol® 130 isoparaffinic solvent in gelatin capsules. A spore suspension of each isolate was then sprayed onto the respective seedlings using a pressure pump connected to a custom-made inoculation device. Inoculations were carried out in an enclosed booth, which was flushed with water between sprays. Standardised procedures for post-inoculation drying of seedlings, dew chamber incubation and greenhouse conditions were followed (Pretorius et al. 2012).

Fresh urediniospores of each isolate were collected from these inoculum multiplications and used for inoculation of 179 germplasm stocks including 160 international triticale entries used in stem rust experiments by Olivera et al. (2013) as well as nine local triticale entries. Control entries included four rye cultivars, one durum wheat cultivar and five wheat cultivars. Leaf rust responses on the primary leaf of seedlings were scored 12 days after inoculation according to the 0 to 4 seedling infection type (SIT) scale described by McIntosh et al. (1995). SIT ratings ranging from 0 to 2+ were considered as resistant and 3 and higher as susceptible. The experiment was repeated to confirm differences observed in SITs between rust isolates.

Temperature sensitivity study

The effect of three different temperature regimes (10 °C, 22.5 °C and 35 °C) on germination percentage as well as on early germ tube elongation of urediniospores of the three leaf rust races and one rye leaf rust isolate was determined. Fresh urediniospores were collected from seedlings of the selective host entries for 3SA144, 3SA145, 3SA248 and UVPr2 15 days post-inoculation. Equal amounts (0.45 mg) of urediniospores of each rust race/isolate were evenly deposited onto water agar plates using a settling tower and air gun as described by Negussie et al. (2005). Nine water agar plates, representing three replicates and three incubation temperatures per isolate, were placed on the rotating base (14 rpm) of the settling tower while the spores were dispersed from the top by using an air gun. After spore release agar plates were exposed for 3 min allowing settling and even distribution of the spores. For 22.5 °C and 35 °C, petri dishes were incubated in growth chambers whereas for the 10 °C incubation a cold room was used. All incubations were done in darkness and temperatures were confirmed using additional thermometers in both growth chambers and the cold room. Spore germination was determined after 3 h of incubation at the respective temperatures. Germination percentage of urediniospores was determined under a microscope by randomly counting a minimum of 100 urediniospores per plate, repeated on three plates per incubation temperature and race/isolate. A spore was considered germinated when the length of the germ tube was equal to the diameter of the spore (Zadoks 1961). The trial was repeated and the number of germinating urediniospores relative to the non-germinating urediniospores was calculated for each trial, treatment and replicate and used in data analysis.

Germ tube elongation was measured by photographing (DP72 Olympus camera) representative fields of germinating urediniospores with cellSens Standard version 1.18 on an Olympus BX53 light microscope (40× magnification). To avoid time delay, photographs were saved and used later to measure early germ tube elongation rate of 20 clearly visible germ tubes, exceeding urediniospore diameter, for each rust entry and temperature combination. Incubation time periods allowed were 2 h at 22.5 °C; 3 h at 10 °C and 4 h at 35 °C. The trial was replicated and the mean germ tube elongation rate per hour was used for data analysis.

Data analysis

Data collected for urediniospore germination were pooled as the two trials did not differ significantly. However, data collected from the two trials conducted for the germ tube elongation rate differed and were analysed separately. Analysis of variance (ANOVA) was conducted on all variables using NCSS Statistical Software (Hintze 2007). Mean separation was conducted using Fisher's unprotected test to determine the least significant difference (LSD) at the 5% significance level.

Results

Seedling infection types

Results of the SIT study are presented in Table S1* with a summary in Table 1 indicating the number of triticale, rye, durum wheat and bread wheat entries susceptible to the respective wheat leaf rust races and the rye leaf rust isolate. Race 3SA144 was the most virulent leaf rust race on triticale with 106 entries being susceptible (SITs ≥3) followed by 3SA248 with 52 and 3SA145 with 49. Except for virulence on three rye cultivars Afgri_1,

Table 1. Summary of the seedling infection type data recorded for 169 triticale, one durum, four rye and five wheat entries to three wheat leaf rust races (3SA144, 3SA145 and 3SA248) and one rye leaf rust field isolate (UVPr2)

Crop	All entries	Leaf rust races/isolate			
		3SA144	3SA145	3SA248	UVPr2
		No. of susceptible entries			
Triticale	169	106	49	52	0
Durum	1	0	1	1	0
Rye	4	0	0	0	3
Wheat	5	0	1	3	0
Total/susceptible entries	179	106	51	56	3

Data presented is a summary of the seedling infection type ratings in Table S1. Infection types ranging from 0 to 2+ were considered as resistant and 3 and higher as susceptible.

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

Arantes and Sorom, UVPr2 was avirulent on all remaining entries with a high number of immune phenotypes.

Although mostly similar SITs were recorded for 3SA145 and 3SA248 they were clearly distinguishable on the triticale entries PI 587268, PI 428933, PI 381429, PI 611876 and PI 507303 (Table S1). The results showed that both 3SA145 and 3SA248 were virulent on triticale entries PI 428740, PI 611789, PI 611797, PI 611874, PI 410804, PI 429068, PI 429072, PI 429297, PI 414960, PI 428855, PI 428823 and PI 428943 whereas 3SA144 was avirulent on these entries. In total 49 out of a possible 169 triticale entries were resistant (SITs ≤2+) to the three wheat leaf rust races.

Germination

ANOVA results for germination percentage indicated a significant ($P < 0.05$) two-way interaction between race and temperature (Table 2). Mean germination percentage of urediniospores for 3SA144, 3SA145, 3SA248 and UVPr2 was >85% when incubated at 22.5 °C, >70% at 10 °C, and ranged from 5.2% (3SA144) to 70.1% (3SA145) when incubated at 35 °C. The lowest mean germination percentage was recorded for the wheat leaf rust race 3SA144 with a mean germination percentage of 61.3% that did not differ from the mean for the rye leaf rust isolate UVPr2 with 62.6%. UVPr2 and 3SA144 appeared to be particularly sensitive to higher temperatures with 28.4% and 5.2% germination, respectively. The races with the highest mean germination percentage were 3SA145 (83.7%) and 3SA248 (84.9%) which did not differ significantly from one another. Based on the ratios of the sum of squares, 63.2% of the variation in mean germination percentage can be attributed to temperature and 17% due to race (data not shown).

Table 2. Two-way interaction between three wheat leaf rust races (3SA144, 3SA145 and 3SA248) and one rye leaf rust field isolate (UVPr2) at three temperatures (°C) on germination percentage (%)

Race/isolate	Temperature (°C)			
	10	22.5	35	Mean
UVPr2	73.4 a	85.9 a	28.4 b	62.6 a
3SA144	87.3 b	91.3 b	5.2 a	61.3 a
3SA145	87.0 b	94.0 bc	70.1 c	83.7 b
3SA248	91.1 c	95.8 c	67.8 c	84.9 b
Mean	84.7 b	91.8 c	42.9 a	73.1

LSD: temperature × race/isolate = 3.18; temperature = 1.59; race/isolate = 1.83.
*Mean values followed by the same letter for each interaction do not differ significantly according to Fishers LSD ($P < 0.05$).

Germ tube elongation rate

ANOVA results of trials one and two for germ tube elongation rate per hour indicated significant differences ($P < 0.05$) due to race and temperature as well as significant two-way interactions ($P < 0.05$) between race and temperature (Table 3). Based on Fisher's

LSD distinct groupings occurred between the lowest and the highest responses. Race 3SA144 differed significantly in its mean germ tube elongation rate in both trials (mean range 39.9 – 42.7 μm/h), over all temperatures, from the other isolates. The highest mean germ tube elongation responses were recorded for UVPr2 (53.1 – 56.6 μm/h), 3SA145 (55.6 – 64.0 μm/h) and 3SA248 (56.7 – 70.4 μm/h) and they did not differ significantly from one another in trial one. In trial two however, significant differences in mean germ tube elongation rate were recorded between the four rust entries over the three temperatures.

Mean germ tube elongation response to temperature, over all races, differed significantly from one another for both trials one and two. The lowest mean response, across trial one and two, was recorded at 35 °C (7.3 and 18.5 μm/h). Almost no measurable germ tubes could be found for 3SA144 at the 35 °C incubation temperature after four hours resulting in a mean of only 0.02 μm/h in both trials. The highest response, across both trials, was recorded at 22.5 °C (91.8 and 96.1 μm/h) followed by 10 °C with a mean range of 57.5 – 58.1 μm/h. Based on the ratios of the sum of squares 91.4% and 80.5% of the variation in mean germ tube elongation can be attributed to temperature and 3.9% and 8.9% due to rust race or isolate, for trial one and two, respectively (data not shown).

Table 3. Two-way interaction between three wheat leaf rust races (3SA144, 3SA145 and 3SA248) and one rye leaf rust field isolate (UVPr2) at three temperatures (°C) on germ tube elongation rate (μm/hour)

Trial 1	Temperature (°C)			
Race/isolate	10	22.5	35	Mean
UVPr2	61.1 b	100.5 c	8.1 b	56.6 b
3SA144	48.1 a	71.4 a	0.02 a	39.9 a
3SA145	60.0 b	97.3 b	9.4 bc	55.6 b
3SA248	60.6 b	98.1 bc	11.5 c	56.7 b
Mean	57.5 b	91.8 c	7.3 a	52.2

LSD: temperature × race/isolate = 2.62; temperature = 1.31; race/isolate = 1.51.

Trial 2	Temperature (°C)			
Race/isolate	10	22.5	35	Mean
UVPr2	56.3 b	82.3 b	20.6 b	53.1 b
3SA144	51.5 a	76.6 a	0.02 a	42.7 a
3SA145	64.3 d	97.0 c	30.7 c	64.0 c
3SA248	60.1 c	128.6 d	22.5 b	70.4 d
Mean	58.1 b	96.1 c	18.5 a	57.6

LSD: temperature × race/isolate = 3.47; temperature = 1.73; race/isolate = 2.00.
*Mean values followed by the same letter for each interaction do not differ significantly according to Fishers LSD ($P < 0.05$).

Discussion

Our study showed that triticale is vulnerable to especially *Pt* race 3SA144, originally collected from triticale, which was virulent to 106 entries. The two *Pt* races 3SA145 and 3SA248 collected from wheat were virulent to 49 and 52 of the triticale entries, respectively. These results support the findings by Hanzalovā and Bartoš (2011) that *Pt* isolates from wheat are less likely to cause disease in triticale, whereas isolates collected from triticale were found more virulent to triticale than wheat. As triticale is mostly planted as a forage crop or cover crop in vineyards in SA and therefore left unsprayed, the increased susceptibility to wheat leaf rust races can contribute to the build-up of inoculum and consequent infection of commercial wheat productions.

The higher virulence found for 3SA144 (SDDN), collected from triticale in the Western Cape SA during 2005, towards the international and local set of triticale germplasm entries is in strong support with earlier findings of increased virulence for this *Pt* race towards triticale (Pretorius and Bender 2010). Using microsatellite analyses, Visser et al. (2011) found that 3SA144, with added virulence for *Lr32*, is closely related to four other South African *Pt* races, namely 3SA132 (SDDJ), 3SA134 (SBD), 3SA137 (SCDS) and 3SA140 (SFDS). Race 3SA145 collected from wheat during the 2009 rust survey season was the first South African *Pt* race with virulence for *Lr37* combined with virulence for *Lr12* and *Lr13* (Terefe et al. 2011). Based on results from microsatellite analyses as well as the avirulence/virulence profile of 3SA145 and the similarity of the latter with other international leaf rust races, Visser et al. (2011) did not exclude the possibility of 3SA145 being an exotic introduction into SA. The avirulence/virulence profile of 3SA248 and supportive microsatellite analyses strongly support the development of this race from 3SA145 (Boshoff et al. 2018). SITs of triticale entries in this study further support this when, except for five entries varying in their resistance to 3SA145 and 3SA248, similar SITs were recorded on the remaining triticale entries.

Results from this study are in support of previous research emphasising the importance of triticale as a source of novel resistance genes in the battle against the rusts of wheat (Olivera et al. 2013). Similarly, it has recently been argued that rye should be further exploited as a source of resistance to wheat pathogens (Crespo-Herrera et al. 2017). The four rye entries included in this study were resistant to the three *Pt* races. Forty-nine triticale accessions showed high levels of seedling resistance to the three wheat leaf rust races. These are considered valuable sources of resistance to wheat leaf rust. The *Pr* isolate UVPr2 was found avirulent on all triticale entries confirming that rust pathogens are highly specialized and can infect mainly one host species.

With average global temperatures on the rise in many regions, recent studies were carried out to determine whether new races of wheat stripe rust, caused by *Puccinia striiformis* Westend. f. sp. *tritici* Erikss. (*Ps*) responsible for epidemic outbreaks, are better adapted to higher temperatures when compared to older races (Milus et al. 2006; Milus et al. 2009; Mboup et al. 2012; Loladze et al. 2014; Tran and Kutcher 2015). Milus et al. (2009) reported that isolates of *Ps* found since 2000 are more aggressive than older isolates with the ability to cause more severe epidemics. They further stated that these "new

isolates" are more adapted to high temperatures with resultant shorter latent periods, faster growth rates and increased spore production. The consequence is that areas with high temperatures, where it was thought that stripe rust might not cause epidemics, have become more favourable environments for disease development (Milus et al. 2009).

From previous studies it is evident that *Pt* is more tolerant over a wide range of environmental conditions when compared to *Ps* (De Vallavieilla-Pope et al. 1995; Singh et al. 2002; Chen 2005). *Pt* therefore attracted less attention in recent studies involving its potential adaptation to warmer temperatures. *In vitro* results from this study showed that the more recently discovered leaf rust races 3SA145 and 3SA248 are better adapted to higher temperatures when compared with the older race 3SA144, which responded almost identical to the different incubation temperatures in both trials. The significantly lower germination percentage recorded for this race at 10 °C and 35 °C in combination with a significant lower germ tube elongation rate at all three temperature regimes is the first report of a lack of comparative adaptation to temperature and early germ tube growth rate for a South African wheat leaf rust race. Although slightly higher trends were observed for 3SA248 in comparison to 3SA145 when mean germination and germ tube elongation rate data are compared, they were more similar in their response and statistically different from the older race 3SA144. Both 3SA145 and 3SA248 showed strong statistical differences and better adaption in their germination and early germ tube growth rate at 35 °C compared to the older race 3SA144. These differences may have contributed to the dominance of 3SA145 (17.9 to 60.5% frequency 2012–2016) in recent rust surveys in SA when compared with 3SA144 (1.6 to 6.7%) (Terefe et al. 2014; Boshoff et al. 2018). To support this statement more of the older SA wheat leaf rust races should be included in future studies.

References

Anikster, Y., Bushnell, W.R., Eilam, T., Manisterski, J., Roelfs, A.P. 1997. *Puccinia recondita* causing leaf rust on cultivated wheats, wild wheats and rye. Can. J. Botany **75**:2082–2096.

Audenaert, K., Troch, V., Landschoot, S., Haesaert, G. 2014. Biotic stresses in the anthropogenic hybrid triticale (× *Triticosecale* Wittmack): current knowledge and breeding challenges. Eur. J. Plant Pathol. **140**:615–630.

Bolton, M.D., Kolmer, J.A., Garvin, D.F. 2008. Wheat leaf rust caused by *Puccinia triticina*. Mol. Plant Pathol. **9**:563–575.

Boshoff, W.H.P., Bender, C.M., Pretorius, Z.A. 2019. Reaction of South African rye, triticale and barley forage cultivars to stem and leaf rust. S. Afr. J. Plant Soil **36(2)**:77–82.

Boshoff, W.H.P., Labuschagne, R., Terefe, T., Pretorius, Z.A., Visser, B. 2018. New *Puccinia triticina* races on wheat in South Africa. Australas. Plant Path. **47**:325–334.

Chai, Y., Kriticos, D.J., Beddow, J.B., Ota, N., Yonow, T., Cuddy, W.S. 2016. *Puccinia triticina*. Harvest Choice Pest Geography. St. Paul, MN: InSTePP-HarvestChoice. pp. 6.

Chen, X.M. 2005. Epidemiology and control of stripe rust (*Puccinia striiformis* f. sp. *tritici*) on wheat. Can. J. Plant Pathol. **27**:314–337.

Crespo-Herrera, L.A., Garkava-Gustavsson, L., Åhman, I. 2017. A systematic review of rye (*Secale cereale* L.) as a source of resistance to pathogens and pests in wheat (*Triticum aestivum* L.). Hereditas **154**:1–9.

De Vallavieille-Pope, C., Huber, L., Leconte, M., Goyeau, H. 1995. Comparative effects of temperature and interrupted wet periods on germination, penetration, and infection of *Puccinia recondita* f. sp. *tritici* and *P. striiformis* on wheat seedlings. Phytopathology **85**:409–415.

Hanzalovā, A., Bartoš, P. 2011. Resistance of triticale to wheat leaf rust (*Puccinia triticina*). Czech J. Genet. Plant **47**:10–16.

Helfer, S. 2014. Rust fungi and global change. New Phytol. **201**:770–780.

Hintze, J. 2007. NCSS 2007. NSCC, LLC. Kaysville, Utah, USA. www.ncss.com.

Huerta-Espino, J., Singh, R.P., German, S., McCallum, B.D., Park, R.F., Chen, W.Q., Bhardwaj, S.C., Goyea, H. 2011. Global Status of wheat leaf rust caused by *Puccinia triticina*. Euphytica **179**:143–160.

Hussain, M., Khan, M.A., Ali, Y., Javaid, M.M., Iqbal, B., Nasir, M., Sabir, W., Muhammad, F. 2017. Wheat breeding for durable rust resistance and high yield potential in historical prospective and current status. Adv. Zool. Bot. **5**:55–63.

Kolmer, J.A., Hughes, M.E. 2018. Physiologic specialization of *Puccinia triticina* on wheat in the United States in 2016. Plant Dis. **102**:1066–1071.

Liu, M., Szabó, L.J., Hambleton, S., Anikster, Y., Kolmer, J.A. 2013. Molecular phylogenetic relationships of the brown leaf rust fungi on wheat, rye, and other grasses. Plant Dis. **97**:1408–1417.

Loladze, A., Druml, T., Wellings, C.R. 2014. Temperature adaptation in Australian populations of *Puccinia striiformis* f. sp. *tritici*. Plant Pathol. **63**:572–580.

Mboup, M., Bahri, B., Leconte, M., De Vallavieille-Pope, C., Kaltz, O., Enjalbert, J. 2012. Genetic structure and local adaption of European wheat yellow rust populations: the role of temperature-specific adaption. Evol. Appl. **5**:341–352.

McIntosh, R.A., Wellings, C.R., Park, R.F. 1995. Wheat rusts: An Atlas of Resistance Genes. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 200.

Meyer, M., Cox, J.A., Hitchings, M.D.T., Burgin, L., Hort, M.C., Hodson, D.P., Gilligan, C.A. 2017. Quantifying airborne dispersal routes of pathogens over continents to safeguard global wheat supply. Nat. Plants **3**:780–786.

Milus, E.A., Kristensen, K., Hovmøller, M.S. 2009. Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis* f. sp. *tritici*. Causing stripe rust of wheat. Phytopathology **99**:89–94.

Milus, E.A., Seyran, E., McNew, R. 2006. Aggressiveness of *Puccinia striiformis* f. sp. *tritici* isolates in the South-Central United States. Plant Dis. **90**:847–852.

Negussie, T., Pretorius, Z.A., Bender, C.M. 2005. Components of rust resistance in lentil. Euphytica **142**:55–64.

Olivera, P.D., Pretorius, Z.A., Badebo, A., Jin, Y. 2013. Identification of resistance to races of *Puccinia graminis* f. sp. *tritici* with broad virulence in triticale (× *Triticosecale*). Plant Dis. **97**:479–484.

Pretorius, Z.A., Ayliffe, M., Bowden, R.L., Boyd, L.A., DePauw, R.M., Jin, Y., Knox, R.E., McIntosh, R.A., Park, R.F., Prins, R., Lagudah, E.S. 2017. Advances in control of wheat rusts. In: P. Langridge (ed.). Achieving sustainable cultivation of wheat. Volume 1: Breeding, quality traits, pests and diseases, Burleigh Dodds Science Publishing, Cambridge, UK. pp. 295–343.

Pretorius, Z.A., Bender, C.M. 2010. First report of virulence for the wheat leaf rust (*Puccinia triticina*) resistance gene *Lr32* in South Africa. Plant Dis. **94**:381.

Pretorius, Z.A., Bender, C.M., Visser, B. 2015. The rusts of wild rye in South Africa. S. Afr. J. Bot. **96**:94–98.

Pretorius, Z.A., Jin, Y., Bender, C.M., Herselman, L., Prins, R. 2012. Seedling resistance to stem rust race Ug99 and marker analysis for *Sr2*, *Sr24* and *Sr31* in South African wheat cultivars and lines. Euphytica **186**:15–23.

Singh, R.P., Huerta-Espino, J., Roelfs, A.P. 2002. The wheat rusts. http://www.fao.org/docrep/006/y4011e/y4011e0g.htm [Accessed 4/06/2018].

Stubbs, R.W., Prescott, J.M., Saari, E.E., Dubin, H.J. 1986. Cereal disease methodology manual. Mexico, D.F.: International Maize and Wheat Improvement Center, CIMMYT. pp. 46.

Terefe, T., Pretorius, Z.A., Bender, C.M., Visser, B., Herselman, L., Negussie, T.G. 2011. First report of a new wheat leaf rust (*Puccinia triticinia*) race with virulence for *Lr12*, *13*, and *37* in South Africa. Plant Dis. **95**:611.

Terefe, T.G., Visser, B., Herselman, L., Prins, R., Negussie, T., Kolmer, J.A., Pretorius, Z.A. 2014. Diversity in *Puccinia triticina* detected on wheat from 2008 to 2010 and the impact of new races on South African wheat germplasm. Eur. J. Plant Pathol. **139**:95–105.

Tran, V.A., Kutcher, H.R. 2015. Temperature effects on the aggressiveness of *Puccinia striiformis* f. sp. *tritici*, stripe rust of wheat. Proceedings of on-line conference proceedings of soils and crops. University of Saskatchewan. www.usask.ca/soilsncrops/conference-proceedings/2015%20pdf/day-1-presentations/room-1-008-tran.pdf

Visser, B., Herselman, L., Bender, C.M., Pretorius, Z.A. 2011. Microsatellite analysis of selected *Puccinia triticina* races in South Africa. Australas. Plant Path. **41**:165–171.

Zadoks, J.C. 1961. Yellow rust on wheat: studies in epidemiology and physiologic specialization. Tijdschr. Planteziekten **67**:69–258.

Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at https://akademiai.com/loi/0806

Electronic Supplementary *Table S1.* Seedling infection types of 169 triticale, one durum, four rye, and five wheat entries to three wheat leaf rust races (3SA144, 3SA145 and 3SA248) and one rye leaf rust field isolate (UVPr2)