

RESEARCH PAPERS

Race structure of *Pyrenophora tritici-repentis* in Morocco

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Summary. The virulence of 135 single-spore isolates of *Pyrenophora tritici-repentis*, collected from durum wheat fields representing most of the major agro-ecological zones of Morocco from 2013 to 2015, was assessed on six international differential wheat genotypes under controlled conditions. Races 1, 5, 6 and 7 were identified with races 5 and 6 being most frequent, representing 47% and 44% of isolates tested, respectively. Only eight isolates (6%) collected at two research stations and a farm field near a station in 2014 and 2015 were race 1, while three isolates collected in 2014 in a farm field in north-eastern Morocco were race 7. The uniform race structure in farm fields may be due to overreliance on a limited and narrow genetic base for durum wheat crops in Morocco. However, the identification of four races is significant since *P. tritici-repentis* can generate new combinations of virulence, thereby increasing race diversity. Combined with the low wheat diversity this may lead to future severe disease epidemics.

Key words: virulence, durum wheat, Morocco.

Introduction

Tan spot, caused by the ascomycete *Pyrenophora tritici-repentis* (Died) (anamorph *Drechslera tritici-repentis*, Died), is one of the most important leaf diseases of durum (*Triticum turgidum*) and bread wheat (*T. aestivum*) (Francl, 1992; Rees *et al.*, 1988; Tekauz *et al.*, 2004). Yield losses as much as 70%, reduced kernel weights, and high degrees of kernel shriveling have been reported after severe tan spot epidemics (Rees *et al.*, 1988). In Morocco, yield losses were shown by Nsarellah *et al.* (2000) to range from 12 to 18% under moderate field infestation levels in the moderately susceptible cultivars grown at the time. *Pyrenophora tritici-repentis* can also infect wheat seed during the grain filling period of crop growth (Schilder and Bergstrom, 1995), causing red or pink smudge which is most detrimental in grain destined for market (Fernández *et al.*, 1994).

Much of the high susceptibility observed in wheat cultivars released after 1960 is associated with the deployment of semi-dwarf wheat germplasm (Rees and Platz, 1982). In Australia, the deployment of toxin-sensitive wheat cultivars was discounted as the main factor to explain emergence of tan spot in that country. This was verified when cultivars developed there since 1911 were tested, and many were found to be susceptible to toxigenic isolates of *P. tritici-repentis* (Oliver *et al.*, 2008). In addition, the increase in tan spot prevalence in recent decades has been associated with conservation tillage practices, short crop rotations, and continuous wheat cultivation (Rees and Platz, 1992; Bailey, 1996; Lamari *et al.*, 2005a).

Initial studies on the variation in virulence in *P. tritici-repentis* based on quantitative approaches (da Luz and Hosford, 1980; Schilder and Bergstrom, 1990) contributed little to the understanding of the *P. tritici-repentis*-wheat interaction. Although some of the studies were comprehensive, most failed to clearly characterize the phenotypic expression of the tan spot syndrome. For example, Shah and Fehrmann

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(1992) did not find physiological races, although significant interactions were detected between host genotypes and pathogen isolates from four geographic locations. A second phase in studies concerned with physiologic specialization in *P. tritici-repentis* is connected to increased understanding of the host-parasite relationships, by defining and characterizing host response phenotypes. Lamari and Bernier (1989b) identified four pathotypes of *P. tritici-repentis* based on their ability to induce tan necrosis and extensive chlorosis (pathotype 1, nec+ chl+), tan necrosis only (pathotype 2, nec+ chl-), extensive chlorosis only (pathotype 3, nec- chl+), or neither symptom (pathotype 4 nec- chl-) on selected host genotypes. Expression of necrosis and chlorosis was shown to be the result of specific interactions between the host and the pathogen. Chlorosis is characterized by the development of diffuse and progressive yellowing of leaves, without tissue degradation. Tan necrosis refers to desiccated tan or yellow-coloured tissue which develops around small dark brown to black leaf spots.

The limitations of this pathotype classification system became evident when isolates of *P. tritici-repentis* from eastern Algeria were found to induce the chlorosis symptom, but on different host genotypes than did the original pathotype 3 isolates (Lamari et al., 1995). Pathotype 3 (currently race 3) had been identified earlier from North America and later the Caucasus region (Lamari et al., 2005b). This race causes chlorosis only on wheat line 6B365 (Lamari et al., 1998; Ali and Francl, 2003; Singh et al., 2007; Aboukhaddour et al., 2013). Isolates from Algeria differed from those originally ascribed to pathotype 3 by their virulence (chlorosis) to cv. Katepwa and line 6B662, and avirulence to line 6B365; the original pathotype 3 isolates are avirulent on cv. Katepwa and 6B662, and virulent on line 6B365. As a consequence, Lamari et al. (1995) and Lamari and Sayoud (1997) proposed the adoption of a race classification system similar to that used for cereal rusts, i.e. based on the virulence of isolates on specific differential wheat genotypes, in addition to the symptom-based pathotype classification system.

Symptom development and physiological variation are mediated by differential production of host-specific toxins by isolates of the fungus, which serve as *P. tritici-repentis* pathogenicity factors (Strelkov and Lamari, 2003). Besides *Stagonospora nodorum*

(Oliver et al., 2012), *P. tritici-repentis* is one of the few documented cases in which a single pathogen produces multiple host-specific toxins that differentially mediate compatibility in different lines or cultivars of a single host species (Lamari et al., 2003).

Presently, eight races of *P. tritici-repentis* have been identified and characterized based on their ability to induce necrosis and/or chlorosis on a differential set composed of four hexaploid wheats, 'Glenlea', 6B365, 6B662 and 'Salamouni', and two tetraploid wheats, 'Coulter' and 4B1149 (Lamari et al., 1995, 1998; Strelkov et al., 2002; Lamari et al., 2003; Strelkov and Lamari, 2003).

Races of *P. tritici-repentis* are defined by their ability or inability to produce at least one of the three toxins identified to date, with 'basic' races producing only a single toxin (race 2, necrosis-inducing ToxA; race 3, chlorosis-inducing ToxC; race 5, chlorosis-inducing ToxB) and 'composite' races which produce multiple toxins (race 1, ToxA+ToxC; race 6, ToxB+ToxC; race 7, ToxA+ToxB; race 8, ToxA+ToxB+ToxC) (Lamari and Strelkov, 2010). Race 4 isolates produce no active toxins and are typically avirulent on wheat.

The race composition of *P. tritici-repentis* has been studied in several geographic regions. In North American collections of the pathogen, Lamari et al. (1995) first identified races 1 to 4, with races 1 and 2 being prevalent (Lamari et al., 1998). Subsequently, these races were also identified from the 'wheat center of diversity' (race 1 in Azerbaijan, Kyrgyzstan, Kazakhstan, Uzbekistan and Syria, race 2 reported only in Azerbaijan and Kazakhstan) (Lamari et al., 2005b), and in South America (Gamba et al., 2012). Races 1 and 4 were reported for the first time in Algeria by Benslimane et al. in 2011. Lamari et al. (1995) were first to report race 5 in Algeria, and this race was subsequently reported from Canada (Strelkov et al., 2002), the United States of America (Ali et al., 1999), Syria, and Azerbaijan (Lamari et al., 2005b). In contrast, race 6 has only been reported from Algeria (Strelkov et al., 2002; Benslimane et al., 2011), while races 7 and 8 have only been found in the Middle East, the Caucasus and Algeria (Lamari et al., 2003, 2005b, Benslimane et al., 2011).

The goal of the present study was to characterize the virulence profile of *P. tritici-repentis* from an extensive collection of isolates from several locations in Morocco, to assess the pathogen race structure in this important North African wheat growing region.

Materials and methods

Fungal isolates

Several surveys were carried out from 2013 to 2015 to collect tan spot-affected plant material. Sites sampled included 31 durum wheat crops in farm fields and experimental material being grown at seven research stations (Annaceur, Jamaa-Shaim, Khemis Zemamra, Merchouch, Allal Tazi, Sidi El Aidi and Tessaout). These locations represent most of the major agro-ecological zones of Morocco as defined by annual rainfall and aridity level (Riad *et al.*, 2013). These zones also represent much of the durum wheat growing area of Morocco. Environmental conditions during the growing seasons in each of 2013, 2014 and 2015 were typical for the agro-ecological zones sampled in the surveys.

Each collection sample consisted of eight to ten leaves showing typical symptoms of tan spot collected randomly either from a commercial crop or from different durum wheat genotypes being grown at research stations. Individual samples were obtained from each of the 31 crops in farm fields, while a total of 36 samples were collected from various durum wheat genotypes being grown at research stations. Wheat growth stages at the time of surveying ranged from beginning of anthesis (ZGS 60) to the milk stage (ZGS 71-73) (Zadoks *et al.*, 1974). At all sites sampled, disease severity ranged from moderate to severe based on the level of symptom development on flag leaves, and host susceptibility and environmental conditions.

Each sample collection was placed into a paper envelope and allowed to air dry at room temperature ($21 \pm 2^\circ\text{C}$) for approx. 24 h. Leaves with visible lesions were cut into 1–2 cm segments and placed in Petri dishes containing lightly moistened filter paper. Fungal sporulation was promoted by incubating the leaf segments at 20°C for 16–20 h under fluorescent light, followed by 16–18 h in the dark at 15°C (Lamari *et al.*, 1995).

From the total of 168 single-spore isolates obtained (representing two to four single-spore isolates per field disease sample), 135 grew well enough in culture to be used for virulence phenotyping on the wheat differential set.

Plant material

The differential set consisted of the six wheat genotypes (Table 1) used by Lamari *et al.* (2003) to characterize the eight known races of *P. tritici-repentis*. Five to seven seeds of each genotype were sown into 15 cm diam. pots filled with growth medium (50:50 peat moss:soil) and kept in a growth chamber at 21°C (day) and 18°C (night) with a 16 h photoperiod.

Inoculation and disease rating

Inoculum of the *P. tritici-repentis* isolates was produced on V8 potato dextrose agar following the procedure described by Lamari and Bernier (1989b). The

Table 1. Reaction phenotypes produced by the four races of *Pyrenophora tritici-repentis* identified in Morocco during 2013–2015 on the six international wheat differentials.

| Host genotype | Race 1 ^a | Race 5 | Race 6 | Race 7 |
|---------------|-----------------------------------|---------|---------|---------|
| 'Glenlea' | 4-5 ^b (N) ^c | 1-2 | 1 | 4-5 (N) |
| 6B365 | 4-5 (C) | 1 | 4-5 (C) | 1 |
| 6B662 | 1 | 4-5 (C) | 5 (C) | 4-5 (C) |
| 'Salamouni' | 1 | 1 | 1 | 1 |
| Coulter | 4-5 (N) | 3-4 (N) | 4-5 (N) | 4-5 (N) |
| 4B1149 | 1 | 1 | 1 | 1 |

^a Races produce the following toxins: race 1, ToxA + ToxC; race 5, ToxB; race 6, ToxB + ToxC and race 7, ToxA + ToxB.

^b Plants were rated on a scale of 1 to 5 based on disease severity, where 1 and 2 represent resistant reactions, and 3 to 5 represent susceptible reactions (Lamari and Bernier, 1989a).

^c (N), necrosis; (C), chlorosis.

conidium suspension of each isolate was adjusted to 3,000 conidia mL⁻¹, with Tween® 20 (polyoxyethylene sorbitol) added to reduce surface tension (one drop per 100 mL). Seedlings were inoculated at the two-leaf stage to run-off with a sprayer set at approx. 67 kPa. After inoculation, the seedlings were moved to a growth chamber having > 90% relative humidity for 24 h at 21°C (day) and 18°C (night), with a 16-h photoperiod, following which they were returned to the previous (plant material) conditions for 6 to 8 d. Tan spot severity was recorded at this time, based on the 1 to 5 scale developed by Lamari and Bernier (1989a), where: 1 = small, dark-brown to black spots, without any surrounding chlorosis or tan necrosis (resistant); 2 = small dark-brown to black spots, with very little chlorosis or tan necrosis (moderately resistant); 3 = small, dark-brown to black spots, completely surrounded by a distinct chlorotic or tan necrotic ring, with lesions generally not coalescing (moderately resistant to moderately susceptible); 4 = small, dark-brown to black spots, completely surrounded with chlorotic or tan necrotic zones; with some of the lesions coalescing (moderately susceptible); and 5 = most lesions consisting of coalescing chlorotic or tan necrotic tissue (susceptible). A water control treatment was included in every run. A randomized complete block experimental design was used, with three replicates (pots) per treatment.

Results

Reaction types on the six wheat differentials host lines corresponded to those exhibited by races 1, 5, 6 and 7 of *P. tritici-repentis* (Table 1). No other races were identified and all isolates were avirulent on 'Salamouni' and 4B1149. Race 1 isolates caused severe necrosis on the differentials 'Glenlea' and 'Coulter' and extensive chlorosis on 6B365, but were avirulent on 6B662, 'Salamouni', and 4B1149. Race 5 isolates induced severe chlorosis only on 6B662, and necrosis only on 'Coulter', but were avirulent on 6B365 'Glenlea', 'Salamouni', and 4B1149. Similarly, race 6 isolates induced extensive chlorosis on 6B365 and 6B662 and necrosis on 'Coulter' but were avirulent on 'Glenlea', 'Salamouni', and 4B1149. Race 7 isolates were also avirulent on 'Salamouni', 4B1149 and 6B365 but induced extensive chlorosis on 6B662 and extensive necrosis on 'Coulter'.

Of the 135 isolates characterized, eight (6%) were classified as race 1; 64 (47%) as race 5; 60 (44%) as

race 6 and three (2%) as race 7 (Table 2). The most prevalent races found in the surveys were 5 and 6, representing 92 % of the isolates. These two races were found in farm fields and at research stations in each of the three years. The only exception was the farm field in Taza, in the Middle Atlas at 1,400 m altitude (Figure 1), which was sampled only in 2014 and where only race 7 was identified (Table 2).

Race 1 was found only at two locations, Annaceur in 2014, in five of the 12 isolates tested (three isolates were race 5 and four were race 6), and at the Merchouch research station in 2014 and 2015 in three of 25 isolates tested (13 were race 5 and nine were race 6) (Table 2). These were the two locations having the greatest race diversity, i.e. where three of the total of four races were detected.

Discussion

To our knowledge, this is the first report characterizing the race structure of *P. tritici-repentis* populations from Morocco. Although four races were identified, races 5 and 6 represented more than 90% of the isolates tested from 2013 to 2015. These two races were found at all locations, except Taza, that was only sampled in 2014. Overall, the virulence diversity in *P. tritici-repentis* in Morocco was less than the highly diverse race composition observed in the wheat centre of diversity, where most known races have been found (Lamari *et al.*, 2005b). This lower level of diversity in Morocco may be due to more than 95% of farm fields being planted to a single tetraploid cultivar, 'Karim', released in 1982 (F. Bassi, personal communication). Races 5 and 6 are both ToxB producers, and this suggests that they are particularly well adapted to this cultivar, which is likely to be sensitive to ToxB. This would provide these races a clear selective advantage. The over-reliance on a limited and narrow genetic base for field wheat crops could lead to severe tan spot epidemics, and would not be unexpected.

The presence of races 5 and 6 in Morocco is not surprising. Race 5 had previously been found in Eastern regions of Algeria (Lamari *et al.*, 1995; Strelkov *et al.*, 2002). This race has also been reported in the United States of America (Ali *et al.*, 1999), Canada (Strelkov *et al.*, 2002), Syria, and Azerbaijan (Lamari *et al.*, 2005). In contrast, race 6 has to date only been identified in Algeria (Strelkov *et al.*, 2002; Benslimane *et al.*, 2011).

The low frequencies of races 1 and 7 (total of eight and three isolates, respectively) can be explained by

Table 2. Race composition of Moroccan populations of *Pyrenophora tritici-repentis* during 2013-2015.

| Location ^a | Climate zone ^b | Year | No. of samples | Race 1 ^c | Race 5 | Race 6 | Race 7 |
|-----------------------|---------------------------|------|----------------|---------------------|-----------|-----------|---------|
| Allal Tazi RS | SH | 2013 | 3 | | 2 (1.5) | 3 (2.2) | |
| Allal Tazi RS | | 2014 | 3 | | 3 (2.2) | 4 (3.0) | |
| Annaceur RS | H | 2013 | 4 | | 2 (1.5) | 5 (3.7) | |
| Annaceur RS | | 2014 | 2 | 1 (0.7) | 1 (0.7) | 3 (2.2) | |
| Annaceur FF | | 2014 | 3 | 4 (3.0) | 2 (1.5) | 1 (0.7) | |
| Bouguedra FF | SA | 2013 | 3 | | 4 (3.0) | 1 (0.7) | |
| Fez FF | SH | 2014 | 1 | | 1 (0.7) | 2 (1.5) | |
| Jamaa-Shaim RS | A | 2013 | 2 | | 3 (2.2) | 2 (1.5) | |
| Jamaa-Shaim FF | | 2013 | 3 | | 2 (1.5) | 4 (3.0) | |
| Khemis Zemamra RS | SA | 2013 | 1 | | 1 (0.7) | 1 (0.7) | |
| Khemis Zemamra FF | | 2013 | 3 | | 3 (2.2) | 3 (2.2) | |
| Labkhathi FF | SA | 2013 | 4 | | 5 (3.7) | 3 (2.2) | |
| Merchouch RS | SA | 2013 | 5 | | 5 (3.7) | 5 (3.7) | |
| Merchouch RS | | 2014 | 6 | 1 (0.7) | 7 (5.2) | 5 (3.7) | |
| Merchouch RS | | 2015 | 6 | 2 (1.5) | 6 (4.4) | 4 (3.0) | |
| Meknes FF | SH | 2014 | 1 | | 1 (0.7) | 1 (0.7) | |
| Safi FF | SA | 2013 | 3 | | 3 (2.2) | 3 (2.2) | |
| Saiss FF | SH | 2013 | 3 | | 2 (1.5) | 3 (2.2) | |
| Sebt Gzoula FF | SA | 2013 | 3 | | 4 (3.0) | 2 (1.5) | |
| Sidi El Aidi RS | SH | 2013 | 2 | | 2 (1.5) | 1 (0.7) | |
| Taza FF | SH | 2014 | 1 | | 0 | 0 | 3 (2.3) |
| Tessaout RS | A | 2015 | 2 | | 1 (0.7) | 2 (1.5) | |
| Zemour FF | SA | 2013 | 3 | | 4 (3.0) | 2 (1.5) | |
| Total | | - | 67 | 8 (5.9) | 64 (47.4) | 60 (44.4) | 3 (2.3) |

^a RS, Research station, FF, Farm field

^b A, arid, annual rainfall (ppt) 251–350 mm; SA, semi-arid, ppt 351–450 mm; SH, sub-humid, ppt 451–550 mm; H, humid, ppt >550 mm.

^c For each race, the value in the first column represents the number of isolates, and the second value represents the percentage of the total number of isolates.

the lack of wheat cultivar diversity in the area surveyed; this might not exert sufficient selection pressure to maintain pathogen virulence factors such as Ptr ToxA and Ptr ToxC. The identification of new or existing races before they become widespread would help to preempt the occurrence of major tan spot epidemics. The detection of race 1 mainly at research stations (Annaceur and Merchouch) is likely due to

the more diverse genetic background of plant material grown there compared to farm fields. As *P. tritici-repentis* can be seed borne (Schilder and Bergstrom, 1995), this indicates the importance of seed health when importing germplasm from other places. Race 1 was also identified in one farm field, in Annaceur, near to the research station. It is possible that it was spread there by wind, since *P. tritici-repentis* can

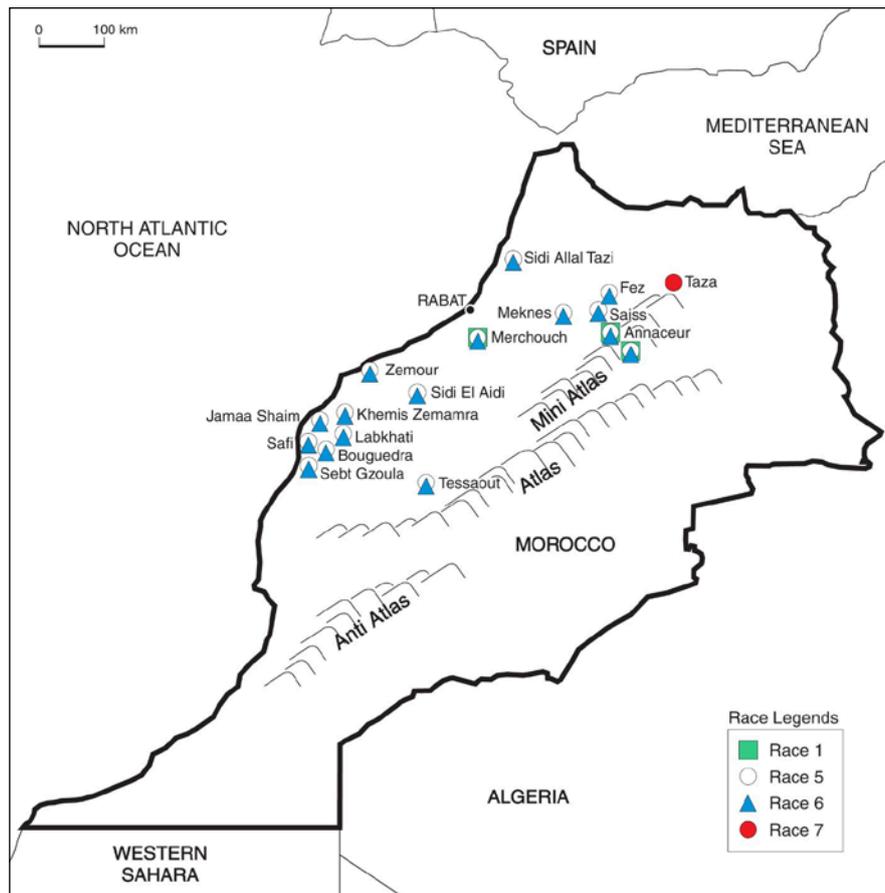


Figure 1. Map of Morocco indicating the locations sampled and the races of *Pyrenophora tritici-repentis* identified from 2013 to 2015 (see Table 2).

be disseminated up to 200 km by wind-blown ascospores (Maraite *et al.*, 1992).

Taza was the only site where race 7 was identified. This site in the Middle Atlas is located 700 km from Maskara (Algeria) where this race had been previously reported (Benslimane *et al.*, 2011). Until the Benslimane *et al.* (2011) study, race 7 had only been identified in the Middle East and the Caucasus (Strelkov *et al.*, 2002; Lamari *et al.*, 2003). The durum cultivar grown in the present study could not be determined, but possibly this was not ‘Karim’, the most widely grown cultivar in Morocco. Alternatively, the *P. tritici-repentis* pathogen population here is more similar to that of Algeria, in comparison to other regions of Morocco.

To date, most isolates of races 5, 6 and 7 of *P. tritici-repentis* have been recovered from tetraploid

wheats, whereas race 1 was regularly found on both hexaploid and tetraploid wheats. However, host ploidy is unlikely to determine specialization in the pathogen, as isolates are grouped on the basis of virulence (Aung, 2001) which is the major force in the specialization and evolution of this fungus.

Nevertheless, although races 1 and 7 were rare, the presence of the four races, 1 (ToxA+ToxC), 5 (ToxB), 6 (ToxB+ToxC), and 7 (ToxA+ToxB) in Morocco represents a continuum of ToxA, ToxB and ToxC production among them, with races differing in their abilities to produce different toxins, and with some races having specific toxins in common. Since *P. tritici-repentis* isolates may carry all combinations of host-selective toxins (Lamari *et al.*, 2003; Strelkov and Lamari, 2003), it is possible that races such as race 8 (ToxA + ToxB + ToxC) that were not

identified in Morocco during this study, may eventually emerge through processes such as sexual recombination.

Overall, tan spot become an increasing threat to wheat production throughout the world over the past few decades. As a necrotrophic pathogen, *P. tritici-repentis* is expected to increase in distribution, infection rate and severity under current global climate change models (Luck *et al.*, 2011). Seed movement of the pathogen should be regarded with caution since it is the most effective means of dispersal, and can have direct impacts on disease management strategies (Brown and Hovmöller, 2002). This is particularly true if the seed originates from a region where the pathogen race composition is different from the destination site where the seed will be grown.

The ultimate goal of race structure studies is to provide practical and significant contributions to plant breeding programmes, such as the Durum Wheat Breeding Program at the International Center of Agricultural Research for the Dry Areas (ICARDA). An objective of this programme is to incorporate effective resistance to tan spot. As such, ongoing studies to monitor changes in the pathogen races present in specific regions are both warranted and necessary. To achieve effective resistance to *P. tritici-repentis*, resistance to both tan necrosis and chlorosis, and to the different toxins should be incorporated into newly developed cultivars. This requires that screening procedures should be based on well-characterized isolates of *P. tritici-repentis* on a qualitative basis, thereby achieving maximum selection efficiency in the development of tan spot-resistant cultivars.

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