Virulence of Egyptian *Blumeria graminis* f. sp. *tritici* Population and Response of Egyptian Wheat Cultivars

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Abstract

Powdery mildew, caused by *Blumeria graminis* (DC.) Speer f. sp. *tritici* (Em. Marchal), is a serious disease of wheat that can cause a large reduction in yield. In Egypt, high powdery mildew severity has been observed in the past few years on many commercial cultivars of both bread and durum wheat. Little information is available about virulence characteristics of the Egyptian *B. graminis* f. sp. *tritici* population in Egypt or the resistance of Egyptian wheat cultivars to powdery mildew. Virulence frequencies of a representative sample of the Egyptian *B. graminis* f. sp. *tritici* population were studied. Seven provinces were chosen to represent the country: two in Upper Egypt (Qena and Sohag), one in Middle Egypt (El Minia), and four in the north (Alexandria, Kafr Elsheikh, Dakahlia, and Sharqia). Ten isolates from each province (70 isolates total) were derived from single ascospores and used for this study. They were inoculated individually

on 21 powdery mildew differential lines, each bearing a single resistance (*Pm*) gene. Also, the responses of 14 Egyptian bread wheat cultivars and 6 durum cultivars to each of the 70 isolates were evaluated individually. Among all tested *Pm* genes, only seven (*Pm1b*, *Pm2*, *Pm21*, *Pm34*, *Pm36*, *Pm37*, and *Pm53*) were effective against *B. graminis* f. sp. *tritici* isolates from all provinces. Several other genes were effective against most or all isolates from a majority of provinces. All tested bread wheat cultivars showed full susceptibility to all isolates, whereas two durum wheat cultivars, Beni-Suef-5 and Beni-Suef-6, had intermediate responses to a large percentage of the isolates, likely indicating partial resistance. To enhance mildew resistance in Egyptian wheat cultivars, it is recommended to use combinations of genes that are nationally effective or effective against multiple provincial *B. graminis* f. sp. *tritici* populations.

In the Mediterranean region and North Africa, bread wheat is one of the most important cereal crops. Durum wheat, with its multiple food uses, is also essential throughout the Mediterranean region, which accounts for about 60% of world durum production (Abad et al. 2004). In Egypt, wheat is an important staple food, with an annual consumption of about 12.4 million tons, of which about 9.4 million tons are grown locally (Rashed et al. 2016) on 1,428,000 ha; about 90% of that is bread wheat and 10% is durum wheat.

Wheat powdery mildew, caused by *Blumeria graminis* (DC.) Speer f. sp. *tritici* (Em. Marchal), can cause severe damage to wheat in various parts of the world. *B. graminis* f. sp. *tritici* is an obligate and host-specific fungal pathogen that colonizes wheat leaves, stem, and spikes and produces a white to gray cottony growth on upper leaf surfaces. When environmental conditions are favorable, powdery mildew may cause partial to total yield loss on susceptible cultivars (Zhang et al. 2015). The disease reduces photosynthesis, increases respiration, reduces root growth, and impedes grain-fill in heavily infected spikes (Akhkha et al. 2003; Last 1962; Sabri et al. 1997). Also, early-season wheat powdery mildew epidemics reduce the number of tillers and the number of kernels per head (Jevtic et al. 1991).

B. graminis f. sp. *tritici* subsists between seasons as chasmothecia (sexual fruiting bodies), which constitute the primary inoculum for the following season (Götz et al. 1996). Ascospores are generally assumed to be released during autumn but that may vary due to weather and environmental conditions (Smedegard-Petersen 1967; Turner 1956).

Although Egyptian researchers and wheat breeders focus largely on breeding for rust resistance, yield, and quality, powdery mildew

can be a significant problem in Egyptian wheat crops grown under higher moisture and fertility conditions. Wheat powdery mildew can spread rapidly in Egypt, given mild temperatures and high humidity during February and March (El-Shamy et al. 2012). Egyptian losses in wheat yield due to powdery mildew may reach 10 to 18% (El-Shamy et al. 2012).

The two principal ways to control wheat powdery mildew are fungicides and cultivars that possess quantitative resistance or major resistance (*Pm*) genes (Leath and Bowen 1989; Leath and Heun 1990; Niewoehner and Leath 1998). As of recently, there were approximately 77 identified alleles at 49 loci conferring resistance to wheat powdery mildew (Hao et al. 2015). In Egypt, the majority of wheat is grown in small fields (<1 ha to several hectares), with each field having a different owner, which reduces fungicide application efficiency. Hence, using resistant cultivars has important advantages for controlling wheat powdery mildew in Egypt.

However, *B. graminis* f. sp. *tritici* has the ability to rapidly overcome resistance genes due to high mutation rates, regular sexual reproduction, and huge effective population sizes. In order to respond to this problem, there is a need for different types of genetic resistance with greater durability (Peusha et al. 2000; Szunics and Szunics 1999), as well as new resistance sources. Wheat breeders use virulence data from mildew population surveys to identify *Pm* genes that may be useful for their breeding programs (Limpert et al. 1987; Niewoehner and Leath 1998).

In Egypt, there have been only two studies involving wheat powdery mildew. One was conducted by El-Shamy et al. (2016), who determined the virulence of *B. graminis* f. sp. *tritici* isolates collected from the north of Egypt. These authors reported high susceptibility of all tested Egyptian cultivars to all *B. graminis* f. sp. *tritici* isolates. The other study was carried out by Emara et al. (2016), who used four simple-sequence repeat markers to detect *Pm* genes in 13 Egyptian cultivars; they concluded that *Pm24*, *Pm35*, and *Pm37* were absent in all the tested cultivars.

More information is required about wheat powdery mildew in Egypt, with respect to both the pathogen population and the resistance available in widely used germplasm. The present investigation aimed to (i) develop a more comprehensive picture of variability for virulence in the *B. graminis* f. sp. *tritici* population across Egyptian

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wheat-growing areas and (ii) evaluate representative Egyptian bread and durum wheat cultivars for their responses to different *B. graminis* f. sp. *tritici* isolates.

Materials and Methods

Sampling of Egyptian *B. graminis* f. sp. *tritici* population. Seventy samples of powdery mildew-infected wheat leaves bearing chasmothecia of *B. graminis* f. sp. *tritici* were collected from wheat fields in seven provinces in Egypt during the 2015–16 growing season (Fig. 1). Infected leaf samples were placed in paper envelopes and sent to Raleigh, NC for derivation of isolates and identification of virulence profiles.

Ascospore ejection and derivation of isolates. The following protocol was used for chasmothecial maturation and ascospore ejection. Filter paper (Whatman International Ltd., Madistone, England) with an 11-cm diameter was cut into strips 2 cm wide, such that a single strip, when pressed into the lid of a small Petri plate (60 by 15 mm), extended out from the lid about 1 cm in each direction. The small Petri plate was then placed in a large Petri plate (100 by 15 mm) containing sterilized water, so that the paper strip ends touched the water and remained moist.

A 2- to 3-cm segment of the infected leaf sample was dipped in 1% bleach (8.25% sodium hypochlorite) for 1 s and rinsed in deionized water. The noninfected side of the leaf was placed on the filter paper strip in the small Petri plate lid, where it adhered due to the moisture, and then the lid with the leaf segment was replaced on its plate in the larger plate of water. The large plate was transferred to a clear plastic

box with a hinged lid, with six large plates per box, and incubated at approximately 17.3°C on a 12-h cycle of light and darkness.

After 7 days, leaf pieces from 10-day-old seedlings of the susceptible wheat cultivar Jagalene (PVP 200200160) were floated on small plates of 0.5% water agar amended with benzimidazole at 50 mg/liter. The lids with the chasmothecia-bearing leaves were placed on the plates containing the Jagalene leaf pieces and incubated at 17 to 18°C with 12 h of light for 24 h. Then, the plates of Jagalene leaf segments were removed, covered with plain lids, and incubated in a growth chamber (approximately 17°C, 12 h of light) for 10 days, until pustules appeared.

As soon as individual pustules were visible, conidia were transferred with a dissecting needle from a single colony onto a fresh leaf piece on a benzimidazole/water agar plate, and incubated in a growth chamber (approximately 17°C, 12 h of light) for 10 days. A second round of subculturing was conducted under the same conditions in order to obtain a pure culture. The cultures obtained from each pustule were subsequently increased for further studies.

Characterization of isolates. In order to analyze virulence, each pure isolate was inoculated on a set of 21 wheat differential lines, each with a single *Pm* gene, plus Jagalene as a susceptible control (Table 1). Some of the genes have long been in use in commercial cultivars, and some were recently introgressed into a common wheat background. One (*Pm36*) was in a durum wheat line.

Experimental units for inoculation were individual Petri plates containing all differential lines and susceptible controls. For replication, all differential plates contained two detached leaves of each differential line; i.e., each plate contained 21 differentials plus the controls.

Fig. 1. Provinces where powdery mildew samples were collected from wheat fields in Egypt during the 2015–16 growing season.

Each isolate was inoculated on two replicate plates of the differentials for a total of four leaf segments per combination of *Pm* gene and isolate.

After inoculation, the plates were incubated for 10 days as described above, then rated for powdery mildew infection as by Parks et al. (2008). Disease severity on each leaf segment was rated 10 days postinoculation using the following scale: 0 = no symptoms, 1 = faint chlorosis, 2 = chlorotic lesion, 3 = necrotic lesion, 4 = chlorotic lesion with mycelium, 5 = one or two pustules with conidia, 6 = <20% coverage with pustules, 7 = 20 to 50% coverage with pustules, 8 = >50% coverage with medium to large pustules, and 9 = approximately 100% coverage with large pustules. Ratings of 0 to 3 were designated as resistant (R), 4 to 6 as intermediate (I), and 7 to 9 as susceptible (S).

Evaluation of Egyptian cultivars. Fourteen Egyptian bread wheat cultivars and six durum wheat cultivars (Table 2) were challenged with each of the *B. graminis* f. sp. *tritici* isolates. The pedigrees of the cultivars were previously published (Draz et al. 2015; Emara et al. 2016; Fahmi et al. 2015; Vavilov Research Institute of Plant Industry 2012). The cultivars represented the most widely grown wheat varieties in Egypt.

Detached leaves from 10-day-old seedlings of the 20 cultivars were arranged in a large plate, along with Jagalene as the susceptible control. For replication, all plates contained two detached leaf segments from each cultivar, and each isolate was inoculated on two replicate plates, for a total of four leaf segments per cultivar-isolate combination. The plates were incubated in a growth chamber (approximately 17°C, 12 h of light) for 10 days, and the cultivars were rated for powdery mildew using the scale described above.

Results

Virulence of isolates. In all, 10 *B. graminis* f. sp. *tritici* isolates were derived from each of the seven Egyptian provinces, for a total of 70 isolates. The responses of each *Pm* gene to the isolates were used to assign the gene to one of three categories, using 0.7 as the minimum proportion of avirulence within a province whereby the gene could be inferred to be effective against that provincial population (Table 3). This level was chosen based on experience in the mid-

Atlantic United States, where wheat powdery mildew epidemics are common and the causal populations have been repeatedly surveyed (Niewoehner and Leath 1998; Parks et al. 2008). Nationally effective *Pm* genes were considered to be those rated as resistant to at least 7 of the 10 isolates from every Egyptian province. Conversely, nationally ineffective genes were those rated as susceptible in response to at least 7 of the 10 isolates from each province. Regionally effective *Pm* genes were those that were effective in some provinces but not others, using the 70% standard.

Seven *Pm* genes were nationally effective: *Pm1b*, *Pm2*, *Pm21*, *Pm34*, *Pm36*, *Pm37*, and *Pm53*. At the other end of the efficacy spectrum, *Pm6*, *Pm8*, and *Pm17* appeared to be defeated throughout the country. The other *Pm* genes varied in their response to particular provincial *B. graminis* f. sp. *tritici* populations; for example, *Pm1a* was effective against the El Minia and Alexandria populations but not those from other provinces.

Of the regionally effective genes, the most widely effective, or those with the highest mean percentages of resistant responses, were *Pm3b*, *Pm4b*, *Pm25*, *NCA6*, and *NCA13* (Table 3). Each of those genes was effective against isolates from all but one or two provinces. Interestingly, with the exception of *Pm4b*, which appears to be defeated only in El Minia, the other four genes in this category were all ineffective in Sharqia, Dakahlia, or both. Sharqia and Dakahlia are near each other in the north of Egypt (Fig. 1), and this similarity suggests mixing of the *B. graminis* f. sp. *tritici* populations in the two provinces.

Resistance of Egyptian wheat cultivars. Fourteen Egyptian bread wheat and six durum wheat cultivars were evaluated against the same set of 70 *B. graminis* f. sp. *tritici* isolates collected from seven Egyptian provinces (Table 4). All bread wheat cultivars showed high susceptibility against almost all tested isolates; only cultivar Gemmiza-12 was resistant to half the isolates each from El Minia and Alexandria. This suggested that none of the evaluated bread wheat cultivars had effective *Pm* genes.

Among the six durum wheat cultivars, Beni-Suef-5, Beni-Suef-6, and Beni-Suef-7 showed a high frequency of partial resistance (PR) to *B. graminis* f. sp. *tritici* isolates collected from the north of Egypt (Alexandria, Kafr Elsheikh, Dakahlia, and Sharqia) (Table 4). The same

Table 1. Powdery mildew differential wheat lines used in virulence analysis of *Blumeria graminis* f. sp. *tritici* isolates from Egypt

Cultivar ^a	Genes ^b	Pedigree	Reference
CI14114	<i>Pm1a</i>	Axminster/8*Chancellor	Sears and Briggie 1969
MocZlatka	<i>Pm1b</i>	ATRI-1509-SLK(TR.MO)/(TR.DR)ATRI-3310-SLK/*Zlatka[1934]	Hsam et al. 1998
CI14118	<i>Pm2</i>	Ulka/8*Chancellor	McIntosh and Baker 1970
CI14120	<i>Pm3a</i>	Asosan/8*Chancellor	Briggie and Sears 1966
CI14121	<i>Pm3b</i>	Chul/8*Chancellor	Briggie and Sears 1966
CI14123	<i>Pm4a</i>	Khapli/8*Chancellor	Ma et al. 2004
Ronos	<i>Pm4b</i>	Graf/Kormoran/Kronjuwel	Yi et al. 2008
Coker 747	<i>Pm6</i>	Arthur/Coker-68-15	Helmsjorgensen and Jensen 1973
Kavkaz	<i>Pm8</i>	Lutescens 314H147/Bezostaja 1	Hsam and Zeller 1997
Amigo	<i>Pm17</i>	Teewon"S"/6/Gaucha/4/Tascosa/3/Wichita/Teewon/5/2*Teewon	Heun et al. 1990
DH2	<i>Pm21</i>	Carries T6VS.6AL from <i>Haynaldia villosa</i>	...
NC96BGTA5	<i>Pm25</i>	Saluda/PI427662 (<i>Triticum monococcum</i>)/Saluda/3/Saluda	Shi et al. 1998
NC96BGTD7	<i>Pm34</i>	Saluda *3/TA2492 (<i>Aegilops tauschii</i>)	Miranda et al. 2006
NC96BGTD3	<i>Pm35</i>	Saluda *3/TA2377 (<i>A. tauschii</i>)	Miranda et al. 2007a
5-BIL29 (durum)	<i>Pm36</i>	Latino *5/MG29896 (<i>T. turgidum</i> ssp. <i>dicoccoides</i>)	Blanco et al. 2008
NC99BGTAG11	<i>Pm37</i>	Saluda *3/ <i>T. timopheevii</i> accession	Perugini et al. 2008
NC09BGTS16	<i>Pm53</i>	Saluda *3/TAU829 (<i>A. speltoides</i>)	Petersen et al. 2015
NC06BGTAG12	<i>MIAG12</i>	Saluda *3/PI 538457 (<i>T. timopheevii</i>)	Maxwell et al. 2009
NC09BGTUM15	<i>MIUM15</i>	Saluda *3/TTCC 223 (<i>A. neglecta</i>)	Worthington et al. 2014
NC96BGTA6	<i>NCA6</i>	Saluda *3/PI 427772 (<i>T. monococcum</i>)	Miranda et al. 2007b
NC06BGTAG13	<i>NCA13</i>	Saluda *3/PI 427442 (<i>T. timopheevii</i>)	Murphy et al. 2007
Jagalene (PI 631376) ^c	None	Jagger/Abilene	...

^a Plant introduction (PI) or cereal investigations (CI) numbers.

^b Powdery mildew resistance (*Pm*) gene or resistance allele.

^c Control.

was true for isolates from Qena province in Upper Egypt, and the three cultivars had somewhat lower PR frequencies to isolates from El Minia and Sohag. In addition, cultivars Sohag-3 and Sohag-5 each showed PR to at least two of the 10 isolates from Qena and Sohag, respectively, while displaying a generally higher frequency of susceptibility to *B. graminis* f. sp. *tritici* isolates collected from the north of Egypt.

Discussion

Our study indicates that relatively few *Pm* genes are widely effective against the Egyptian *B. graminis* f. sp. *tritici* population. Only seven resistance genes (*Pm1b*, *Pm2*, *Pm21*, *Pm34*, *Pm36*, *Pm37*, and *Pm53*) were effective against the population as sampled broadly across Egypt. However, other genes still have efficacy in some regions, and may still be useful when pyramided. This is the first study to determine the response of *Pm1b*, *Pm21*, *Pm34*, and *Pm53* to the *B. graminis* f. sp. *tritici* population in Egypt.

We first discussed the genes that appear to be partially or completely ineffective in Egypt. *Pm1a* was reported as completely ineffective in all sampled locations by El-Shamy et al. (2016) during the 2013–2014 growing season; however, our isolates from previously unsampled regions indicated that *Pm1a* is likely still effective in Alexandria in the north and El Minia in middle Egypt.

High virulence to *Pm3a* and *Pm3b* had been found in the United States (Niewoehner and Leath 1998; Parks et al. 2008) but low virulence in western Europe (Clarkson and Slater 1999) and Morocco (Imani et al. 2002). For Egypt, we categorized *Pm3a* and *Pm3b* as regionally effective (Table 3). By contrast, El-Shamy et al. (2016) reported *Pm3a* as a defeated gene in Egypt; significant virulence was found at only one location (Dakahlia) common to both their study and ours. We found that *Pm3a* is also likely effective in the other previously unsampled regions of Alexandria, Kafr Elsheikh, El Minia, and Qena, as is *Pm3b*.

Pm6, *Pm8*, and *Pm17* were ineffective against Egyptian *B. graminis* f. sp. *tritici* isolates in our seedling assay. *Pm6* and *Pm17* may express partial resistance in the adult stage (El-Shamy et al. 2016) but *Pm8* cannot be recommended as a source of resistance. The similarity in responses of *Pm8* and *Pm17* to *B. graminis* f. sp. *tritici* isolates

may be due to their common origin, with both genes originating from rye (*Secale cereale*) (Niewoehner and Leath 1998). Interestingly, *Pm8* has lost its efficacy against *B. graminis* f. sp. *tritici* not only in Egypt but also on the Atlantic coast in Morocco (Imani et al. 2002); in Europe (Hsam and Zeller 2002), including Hungary (Komáromi and Vida 2009); and China (Wang et al. 2005). In the eastern United States, commercial cultivars with *Pm8* have long been in common use (Niewoehner and Leath 1998); however, the gene began to exhibit breakdown in some regions in 2003 to 2005 (Parks et al. 2008), and was defeated in the Great Plains and all eastern U.S. regions by 2014 (Cowger et al. 2017).

Turning to the genes that appear to be nationally effective in Egypt, we begin with *Pm1b*. To our knowledge, this was the first time *Pm1b* was tested against Egyptian *B. graminis* f. sp. *tritici* isolates. Unlike *Pm1a*, to which both our study and the previous one by El-Shamy et al. (2016) recorded widespread virulence, *Pm1b* showed high resistance against all the presently tested isolates. *Pm1b* is a resistance allele transferred into the common wheat cultivar MocZlatka from *Triticum monococcum* (Hsam et al. 1998). Due to its efficacy, it is recommended as an effective resistance gene in Egypt.

In Morocco, virulence frequencies to *Pm2* were intermediate (Imani et al. 2002), whereas high virulence to *Pm2* has been reported in Europe and the eastern United States; and, in Hungary, the frequency of virulence was over 90% (Komáromi and Vida 2009). By contrast, in the present study, *Pm2* was effective against most Egyptian isolates. The regional differences are likely due to a relative absence of *Pm2* in recent Egyptian cultivars and, thus, the lack of selection pressure.

Pm21 has been effective in many parts of the world, including Poland, China, and Europe (Chen et al. 1995; Czembor et al. 2014; Huang et al. 1997; Liu et al. 2015). Transferred to common wheat from *Haynaldia* (= *Dasypyrum*) *villosum*, a wild wheat relative, via a translocation (6VS.6AL), this gene has been widely used in breeding (He et al. 2016) and was recently made accessible to breeders in a spring-habit background (Lukaszewski and Cowger 2017). In our study, *Pm21* was completely effective against all *B. graminis* f. sp. *tritici* isolates from Egypt, and it should be useful in common wheat breeding programs there.

Table 2. Egyptian wheat cultivars tested against 70 powdery mildew isolates collected from seven provinces in Egypt

Cultivar	Pedigree	References
Bread wheat		
Shandaweel-1	Site//MO/4/NAC/TH.AC//3*PVN/3/Mirlo/Buc	Draz et al. 2015
Misr-1	Oasis/Skauz//4*BCN/3/2*Pastor	Draz et al. 2015
Misr-2	Skauz/BAV92	Draz et al. 2015
Sids-12	BUC//7c/Ald/5/Maya 74/On/1160.147/3/BB/GLL/4/Chat''S''/6/Maya/vu1//Cmh 74A.630//4*sx	Draz et al. 2015
Sids-13	Almaz19 = Kauz "S"/TSI/SNB"S"	Draz et al. 2015
Sids-14	SW8488*2/Kukuna-CGSS01Y00081T-099M-099Y-099M-099B-9Y-0B-0SD	Emara et al. 2016
Sakha-93	Sakha 92/TR 810328 S 8871-1S-2S-1S-0S	Imbasy et al. 2014
Sakha-94	Opata/Rayon/Kauz. CMBW90Y3280-0TOPM-3Y-010M-010M-010Y-10M-015Y-0Y	Draz et al. 2015; Imbasy et al. 2014
Gemmiza-9	Ald"S"/Haus//CMH74A.630/SxCGM4583-5GM-1GM-0GM	Imbasy et al. 2014
Gemmiza-10	Maya74"S"/ON/1160-147/3/Bb/G11/4/chat"S"/5/crow"S"/CGM5820- 3GM-1GM-2GM-0GM	Imbasy et al. 2014
Gemmiza-11	B0W"S"/KVZ"S"/7C/SERI82/3/Giza168/Sakha61. GM7892-2GM-1GM-2GM-1GM-0GM	Draz et al. 2015
Gemmiza-12	OTS/3/Sara/THB//vee-CMss97Y0027S-5Y-010M-010Y-010M-2Y-1M-0Y-06M-06M-0GM	Emara et al. 2016
Giza-168	Mil/Buc//Seri CM93046-8M-0Y-0M-2Y-0B	Draz et al. 2015
Giza-171	Gemmiza-9/Sakha-93	Emara et al. 2016
Durum wheat		
Beni-Suef-4	Dipper/Bushen-3	Draz et al. 2015
Beni-Suef-5	Dipper-2/Bushen-3	Fahmi et al. 2015
Beni-Suef-6	Boomer-21/Busca-3	Vavilov Research Institute of Plant Industry 2012
Beni-Suef-7	In registration process	
Sohag-3	Mexi"S"/Mgha/51792//Durum6	Fahmi et al. 2015
Sohag-5	In registration process	...

Table 3. Virulence of *Blumeria graminis* f. sp. *tritici* isolates collected from seven Egyptian provinces to wheat powdery mildew (*Pm*) resistance genes^a

Genes ^b	Upper Egypt						Middle Egypt			Northern Egypt												Mean		
	Qena			Sohag			El Minia			Alexandria			Kafr Elsheikh			Dakahlia			Sharqia					
	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R			
Nat eff																								
<i>Pm1b</i>	3	0	7	2	0	8	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0.7	0	9.3
<i>Pm2</i>	3	0	7	2	0	8	0	0	10	0	0	10	0	0	10	0	0	10	0	1	9	0.7	0.2	9.1
<i>Pm21</i>	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0.0	0.0	10.0
<i>Pm34</i>	1	1	8	1	2	7	0	0	10	0	1	9	0	0	10	1	1	8	1	2	7	0.6	1	8.4
<i>Pm36</i>	0	0	10	0	2	8	0	0	10	0	1	9	0	0	10	0	0	10	0	0	10	0.0	0.4	9.6
<i>Pm37</i>	0	0	10	0	2	8	0	0	10	0	0	10	0	0	10	0	3	7	0	1	9	0.0	0.9	9.1
<i>Pm53</i>	0	1	9	0	1	9	0	0	10	0	0	10	0	1	9	0	0	10	0	1	9	0.0	0.6	9.4
Nat inef																								
<i>Pm6</i>	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	8	2	0	10	0	0	9.7	0.3	0.0
<i>Pm8</i>	10	0	0	10	0	0	7	2	1	6	0	4	10	0	0	10	0	0	10	0	0	9	0.3	0.7
<i>Pm17</i>	9	0	1	7	0	3	10	0	0	7	3	0	9	1	0	10	0	0	9	0	1	8.7	0.6	0.7
Reg eff																								
<i>Pm1a</i>	7	0	3	7	0	3	1	0	9	0	0	10	8	0	2	10	0	0	10	0	0	6.1	0	3.9
<i>Pm3a</i>	2	0	8	7	1	2	0	1	9	0	2	8	1	1	8	5	1	4	6	2	2	3	1.1	5.9
<i>Pm3b</i>	0	0	10	2	2	6	0	1	9	0	0	10	1	0	9	5	1	4	3	1	6	1.6	0.7	7.7
<i>Pm4a</i>	0	0	10	10	0	0	9	1	0	8	0	2	1	0	9	1	1	8	0	0	10	4.1	0.3	5.6
<i>Pm4b</i>	0	0	10	0	0	10	10	0	0	1	0	9	1	1	8	0	1	9	0	1	9	1.7	0.4	7.9
<i>Pm25</i>	1	2	7	0	1	9	2	0	8	0	0	10	0	0	10	1	5	4	2	3	5	0.9	1.6	7.5
<i>Pm35</i>	3	4	3	1	4	5	8	1	1	1	4	5	1	3	6	0	8	2	1	7	2	2.2	4.4	3.4
<i>MIAG12</i>	1	3	6	0	2	8	0	0	10	0	0	10	0	1	9	3	6	1	4	1	5	1.1	1.9	7.0
<i>MIUM15</i>	7	0	3	7	0	3	1	1	8	0	0	10	8	0	2	10	0	0	10	0	0	6.1	0.2	3.7
<i>NCA6</i>	1	0	9	0	3	7	0	0	10	0	0	10	0	0	10	1	2	7	0	4	6	0.3	1.3	8.4
<i>NCAG13</i>	1	1	8	0	3	7	0	0	10	0	0	10	0	1	9	4	1	5	3	4	3	1.1	1.4	7.4
Jagalene	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0

^a Ten isolates were tested for each combination of province and *Pm* gene; values are numbers of isolates. S = susceptible (rating of 7 to 9), I = intermediate (rating of 4 to 6), and R = resistant (0 to 3). *Pm* genes were categorized as "effective" if ≥ 7 of the 10 isolates from a province were avirulent to them.

^b Nat eff = nationally effective, Nat inef = nationally ineffective, and Reg eff = regionally effective genes.

Table 4. Response of 20 Egyptian wheat cultivars to 70 Egyptian *Blumeria graminis* f. sp. *tritici* isolates^a

Cultivar	Upper Egypt						Middle Egypt			Northern Egypt												Mean		
	Qena			Sohag			El Minia			Alexandria			Kafr Elsheikh			Dakahlia			Sharqia					
	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R	S	I	R
Bread wheat																								
Shandaweel-1	10	0	0	10	0	0	3	1	6	5	0	5	10	0	0	10	0	0	10	0	0	8.3	0.1	1.6
Misr-1	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Misr-2	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Sids-12	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Sids-13	10	0	0	10	0	0	10	0	0	9	1	0	9	1	0	10	0	0	10	0	0	9.7	0.3	0.0
Sids-14	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Sakha-93	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Sakha-94	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Gemmiza-9	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Gemmiza-10	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Gemmiza-11	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Gemmiza-12	10	0	0	10	0	0	3	2	5	5	0	5	10	0	0	10	0	0	10	0	0	8.3	0.3	1.4
Giza-168	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Giza-171	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0
Durum wheat																								
Beni-Suef-4	10	0	0	10	0	0	10	0	0	9	1	0	10	0	0	10	0	0	10	0	0	9.9	0.1	0.0
Beni-Suef-5	0	7	3	8	2	0	4	6	0	0	8	2	0	6	4	1	9	0	0	9	1	1.9	6.7	1.4
Beni-Suef-6	0	8	2	8	2	0	6	4	0	1	9	0	0	8	2	0	8	2	0	10	0	2.1	7.0	0.9
Beni-Suef-7	5	5	0	5	5	0	6	4	0	4	6	0	1	8	1	2	8	0	2	8	0	3.6	6.3	0.1
Sohag-3	5	5	0	7	3	0	10	0	0	10	0	0	9	1	0	10	0	0	10	0	0	8.7	1.3	0.0
Sohag-5	8	2	0	8	2	0	10	0	0	9	1	0	9	1	0	7	3	0	9	1	0	8.6	1.4	0.0
Jagalene	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10	0	0	10.0	0.0	0.0

^a Ten isolates were tested for each combination of province and wheat cultivar; values are numbers of isolates. S = susceptible (rating of 7 to 9), I = intermediate (rating of 4 to 6), and R = resistant (0 to 3).

Four genes recently introduced into cultivated wheat performed well in response to Egyptian *B. graminis* f. sp. *tritici* isolates from all provinces. *Pm34* is recommended for pyramiding in U.S. wheat germplasm by Miranda et al. (2006) due to its efficacy against U.S. *B. graminis* f. sp. *tritici* isolates. Blanco et al. (2008) transferred *Pm36* from *T. turgidum* var. *dicoccoides* into durum wheat by backcrossing, and the gene previously performed well against Egyptian powdery mildew (El-Shamy et al. 2016). The efficacy of *Pm36* was confirmed in our study, and it can be recommended for both common and durum wheat breeding programs. *Pm37* is a dominant gene and mapped on the long arm of chromosome 7A (Perugini et al. 2008); it is highly effective against the U.S. *B. graminis* f. sp. *tritici* population. *Pm53* was recently mapped to chromosome 5BL and showed good efficacy against powdery mildew from the United States (Petersen et al. 2015).

We found that, in response to the majority of *Pm* genes tested, the provincial samples of *B. graminis* f. sp. *tritici* varied in frequency of virulence, with some local populations largely virulent to a specific gene while others were largely avirulent. These results indicate that the Egyptian *B. graminis* f. sp. *tritici* population is genetically diverse, and suggest that it is locally subdivided. The *Pm* genes that were regionally effective but evoked high avirulence frequencies across the largest number of provinces and, thus, could potentially be useful in breeding, especially in combination, were *Pm3b*, *Pm4b*, *Pm25*, *NCA6*, *MIAG12*, and *NCAG13*.

Our study also indicates that there is little to no major-gene resistance to wheat powdery mildew in existing Egyptian commercial wheat germplasm. This includes Misr-1, Misr-2, and others considered the Egyptian cultivars most resistant to cereal rusts. *Pm21*, *Pm 34*, *Pm36*, *Pm37*, and *Pm53* are promising sources of major-gene resistance that is effective against the Egyptian *B. graminis* f. sp. *tritici* population and beyond. Egyptian wheat breeding programs should add the introgression of powdery mildew resistance to the set of priority traits, along with rusts and yield quality and quantity, for which new genetic resources are sought. A strategy to introgress and pyramid *Pm* genes will be more effective and durable if adult-plant (partial) resistance and quantitatively resistant genetic backgrounds are also utilized. In the United States, several genes confer adult-plant (slow-mildewing) resistance, including *Pm3e*, *Pm3f*, *Pm3g*, *Pm4a*, *Pm5b*, and *Pm7* (C. Cowger, personal observation), and these may also be useful in Egypt.

Although the bread wheat cultivars in this study were uniformly susceptible, some of the Beni-Suef durum cultivars had high levels of intermediate resistance as seedlings, particularly to northern Egyptian *B. graminis* f. sp. *tritici* populations. That is likely because, in Middle and Upper Egypt, durum is more commonly cultivated than bread wheat, especially the Beni-Suef cultivars, including Beni-Suef-5 and Beni-Suef-6. This pattern of cultivation probably selected the pathogen population for full virulence to these cultivars, in contrast to the north, where the pathogen has adapted primarily to bread wheat cultivars.

In conclusion, there is a need to incorporate effective *Pm* genes such as *Pm1b*, *Pm2*, *Pm21*, *Pm 34*, *Pm36*, *Pm37*, and *Pm53* into Egyptian bread and durum wheat genotypes. Gene pyramids will be important to guard against rapid defeat of individual genes by *B. graminis* f. sp. *tritici* evolution. Also, Beni-Suef-5 and -6 likely have effective partial resistance against *Pm* isolates from Egypt and are good material for that purpose in durum wheat breeding programs.

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