



## Research

## Crop Genetics and Breeding—Perspective

# The Potential Role of Powdery Mildew-Resistance Gene *Pm40* in Chinese Wheat-Breeding Programs in the Post-*Pm21* Era

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## ABSTRACT

Powdery mildew, which is caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is an important leaf disease that affects wheat yield. Powdery mildew-resistance (*Pm*) gene *Pm21* was first transferred into wheat in the 1980s, by translocating the *Heuchera villosa* chromosome arm 6VS to the wheat chromosome arm 6AL (6VS-6AL). Recently, new *Bgt* isolates that are virulent to *Pm21* have been identified in some wheat fields, indicating that wheat breeders should be aware of the risk of deploying *Pm21*, although pathological details regarding these virulent isolates still remain to be discovered. *Pm40* was identified and mapped on the wheat chromosome arm 7BS from several wheat lines developed from the progenies of a wild cross between wheat and *Thinopyrum intermedium*. *Pm40* offers a broad spectrum of resistance to *Bgt*, which suggests that it is likely to provide potentially durable resistance. Cytological methods did not detect any large alien chromosomal segment in the wheat lines carrying *Pm40*. Lines with *Pm40* and promising agronomical traits have been released by several wheat-breeding programs in the past several years. Therefore, we believe that *Pm40* will play a role in powdery mildew-resistance wheat breeding after *Pm21* resistance is overcome by *Bgt* isolates. In addition, both *Pm21* and *Pm40* were derived from alien species, suggesting that the resistance genes derived from alien species are potentially more durable or effective than those identified from wheat.

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## 1. Introduction

Wheat powdery mildew, which is caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is a destructive fungal disease around the world, and remains a significant threat to wheat (*Triticum aestivum* L. (*T. aestivum* L.)) production. In China, wheat powdery mildew has been widespread in most winter wheat-growing regions since the 1970s, and has caused severe yield losses [1]. In southwest China, although powdery mildew was second to stripe rust (caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*)) in the past, it now surpasses stripe rust as the most destructive wheat leaf disease due to the deployment of semi-dwarf cultivars and the increased use of irrigation and nitrogenous fertilizers [2–4].

Chemical control and appropriate wheat-cultivation measures can reduce some of the yield losses caused by powdery mildew; however, growing new disease-resistant cultivars is the best

strategy for controlling powdery mildew and will also reduce both the production cost and the environmental contamination from the application of fungicides [5]. Powdery mildew-resistance (*Pm*) genes are the prerequisite for developing resistant wheat cultivars; therefore, the identification of new *Pm* genes is an important ongoing task for breeders in order to improve wheat resistance to powdery mildew. To date, 91 *Pm* genes (*Pm18* = *Pm1c*, *Pm22* = *Pm1e*, *Pm23* = *Pm4c*, *Pm17* = *Pm8*, *Pm31* = *Pm21*, and *Pm48* = *Pm46*) [6–12] have been identified on 54 loci of wheat chromosomes (Table 1) [1,4,6–10,12–78]. *Pm* genes have been assigned on almost all chromosomes except 3D and 4D. The number of loci on the B genome is up to 27 (50.0%) out of 54 loci, while the number of loci on the D genome is only 13 (24.1%) (Table 2). The number of *Pm* genes mapped on the A genome is up to 42 (46.2%), whereas only 17 (18.7%) *Pm* genes are mapped on the D genome. The mean number of *Pm* alleles per loci is 3.00, 1.19, and 1.31 in the A, B, and D genomes, respectively, which shows that each *Pm* locus in the A genome has more alleles than those in the B and D genome. Moreover, the data in Table 2 show that the alien *Pm* genes such as *Pm21* and *Pm40*, usually displaying

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**Table 1**  
Powdery mildew-resistance genes reported in wheat and their chromosomal distribution.

Chromosome	Locus	Genes from <i>T. aestivum</i>	Genes from alien species
1A	<i>Pm3</i> , <i>Pm25</i>	<i>Pm3a</i> [13], <i>Pm3b</i> [13], <i>Pm3c</i> [14], <i>Pm3d</i> [15], <i>Pm3e</i> [15], <i>Pm3f</i> [15], <i>Pm3g</i> [16], <i>Pm3h</i> [16], <i>Pm3i</i> [16], <i>Pm3j</i> [16], <i>Pm3l</i> [17], <i>Pm3m</i> [18], <i>Pm3n</i> [18], <i>Pm3o</i> [18], <i>Pm3p</i> [18], <i>Pm3q</i> [18], <i>Pm3r</i> [18]	<i>Pm3k</i> ( <i>T. turgidum dicoccon</i> ) [17], ( <i>Secale cereale</i> ( <i>S. cereale</i> )) [19], <i>Pm25</i> ( <i>T. boeoticum</i> ) [20]
2A	<i>Pm4</i> , <i>Pm50</i>	<i>Pm4c</i> ( <i>Pm23</i> ) [9], <i>Pm50</i> [21]	<i>Pm4a</i> ( <i>T. dicoccum</i> ) [14,22], <i>Pm4b</i> ( <i>T. carthlicum</i> ) [23,24], <i>Pm4d</i> ( <i>T. monococcum</i> ) [25]
3A	<i>Pm44</i>	<i>Pm44</i> [26]	
4A	<i>Pm16</i>		<i>Pm16</i> ( <i>T. dicoccoides</i> ) [27]
5A	<i>Pm55</i>		<i>Pm55</i> (5AL/5DL) ( <i>Dasyphyrum villosa</i> ) [28]
6A	<i>Pm21</i> , <i>Pm56</i>		<i>Pm21</i> ( <i>Pm31</i> ) ( <i>Haynaldia villosa</i> ) [29,30], <i>Pm56</i> ( <i>S. cereale</i> ) [116]
7A	<i>Pm1</i> , <i>Pm9</i> , <i>Pm37</i> , <i>Pm59</i> , <i>Pm60</i>	<i>Pm1a</i> [31,32], <i>Pm1c</i> ( <i>Pm18</i> ) [7,33], <i>Pm1e</i> ( <i>Pm22</i> ) [8], <i>Pm9</i> [34], <i>Pm59</i> [117]	<i>Pm1b</i> ( <i>T. monococcum</i> ) [7], <i>Pm1d</i> ( <i>Aegilops speltoides</i> ( <i>Ae. speltoides</i> )) [7], <i>Pm37</i> ( <i>T. timopheevi</i> ) [35], <i>Pm60</i> ( <i>T. urartu</i> ) [81]
1B	<i>Pm8</i> , <i>Pm28</i> , <i>Pm32</i> , <i>Pm39</i>	<i>Pm28</i> [36], <i>Pm39</i> [37]	<i>Pm8</i> ( <i>Pm17</i> ) ( <i>S. cereale</i> ) [10], <i>Pm32</i> ( <i>Ae. speltoides</i> ) [38]
2B	<i>Pm6</i> , <i>Pm26</i> , <i>Pm33</i> , <i>Pm42</i> , <i>Pm49</i> , <i>Pm51</i> , <i>Pm52</i> , <i>Pm57</i>	<i>Pm52</i> [1]	<i>Pm6</i> ( <i>T. timopheevi</i> ) [39,40], <i>Pm26</i> ( <i>T. dicoccoides</i> ) [41], <i>Pm33</i> ( <i>T. carthlicum</i> ) [42], <i>Pm42</i> ( <i>T. turgidum dicoccon</i> ) [43], <i>Pm49</i> ( <i>T. turgidum dicoccon</i> ) [44], <i>Pm51</i> ( <i>Thinopyrum ponticum</i> ( <i>Th. ponticum</i> )) [45], <i>Pm57</i> ( <i>Ae. searsii</i> ) [46]
3B	<i>Pm13</i> , <i>Pm41</i>		<i>Pm13</i> ( <i>Ae. longissima</i> ) [47], <i>Pm41</i> ( <i>T. turgidum dicoccon</i> ) [48]
4B	<i>Pm7</i>		<i>Pm7</i> ( <i>S. cereale</i> ) [49,50]
5B	<i>Pm30</i> , <i>Pm36</i> , <i>Pm53</i>		<i>Pm30</i> ( <i>T. dicoccoides</i> ) [51], <i>Pm36</i> ( <i>T. turgidum dicoccon</i> ) [52], <i>Pm53</i> ( <i>Ae. speltoides</i> ) [53]
6B	<i>Pm11</i> , <i>Pm12</i> , <i>Pm14</i> , <i>Pm20</i> , <i>Pm27</i> , <i>Pm54</i>	<i>Pm11</i> [54], <i>Pm14</i> [55], <i>Pm54</i> [56]	<i>Pm12</i> ( <i>Ae. speltoides</i> ) [57], <i>Pm20</i> ( <i>S. cereale</i> ) [49], <i>Pm27</i> ( <i>T. timopheevii</i> ) [58]
7B	<i>Pm5</i> , <i>Pm40</i> , <i>Pm47</i>	<i>Pm5c</i> [59], <i>Pm5d</i> [59,60], <i>Pm5e</i> [61], <i>Pm47</i> [62]	<i>Pm5a</i> ( <i>T. dicoccum</i> ) [63], <i>Pm5b</i> ( <i>T. dicoccum</i> ) [59], <i>Pm40</i> ( <i>Th. intermedium</i> ) [4,64]
1D	<i>Pm10</i> , <i>Pm24</i>	<i>Pm10</i> [65], <i>Pm24a</i> [66,67], <i>Pm24b</i> [68]	
2D	<i>Pm43</i> , <i>Pm58</i>		<i>Pm43</i> ( <i>Th. intermedium</i> ) [69], <i>Pm58</i> ( <i>Ae. tauschii</i> ) [6]
5D	<i>Pm2</i> , <i>Pm34</i> , <i>Pm35</i> , <i>Pm46</i>	<i>Pm2c</i> [70,71], <i>Pm46</i> ( <i>Pm48</i> ) [12]	<i>Pm2a</i> ( <i>Ae. tauschii</i> ) [72,73], <i>Pm2b</i> ( <i>Agropyron cristatum</i> ) [70], <i>Pm34</i> ( <i>Ae. tauschii</i> ) [74], <i>Pm35</i> ( <i>Ae. tauschii</i> ) [75]
6D	<i>Pm45</i>	<i>Pm45</i> [76]	
7D	<i>Pm15</i> , <i>Pm19</i> , <i>Pm29</i> , <i>Pm38</i>	<i>Pm15</i> [55], <i>Pm38</i> [77]	<i>Pm19</i> ( <i>Ae. squarrosa</i> ) [72,73], <i>Pm29</i> ( <i>Ae. ovate</i> ) [78]

**Table 2**  
The different distributions of formally named powdery mildew-resistance genes on wheat A, B, and D genomes.

Genome	Number of loci	Number of <i>Pm</i> genes (genes from alien species)	Proportion of alien genes	Mean number of alleles per average locus
A	14	42 (14)	0.33	3.00
B	27	32 (22)	0.69	1.19
D	13	17 (8)	0.47	1.31

the board-spectrum and putatively durable resistance, were frequently transferred from wild relatives into A and B genome.

## 2. The contribution of alien *Pm* genes to the improvement of wheat resistance to powdery mildew

The transfer of desirable alien genes from wild relatives with durable resistance to a broad spectrum of pathogens into wheat is an important objective in modern breeding programs [79]. Within the 54 named *Pm* genes, 44 genes in 37 loci were derived from wild relatives or sparsely cultivated subspecies. These include *T. boeoticum* (*Pm25*) [20], *T. monococcum* (*Pm1b* and *Pm4d*) [7,25], *T. dicoccoides* (*Pm16*, *Pm26*, *Pm30*, and *Pm31*) [27,29,41,51], *T. dicoccum* (*Pm4a*, *Pm5a*, and *Pm5b*) [59,63,80], *T. carthlicum* (*Pm4b* and *Pm33*) [23], *T. turgidum dicoccon* (*Pm3k*, *Pm36*, *Pm41*, *Pm42*, and *Pm49*) [17,43,44,48,52], *T. timopheevi* (*Pm6*, *Pm27*, and *Pm37*) [35,39,58], *T. urartu* (*Pm60*) [81], *A. cristatum* (*Pm2b*) [70], *Aegilops* spp. (*Pm1d*, *Pm2a*, *Pm12*, *Pm13*, *Pm19*, *Pm29*, *Pm32*, *Pm34*, *Pm35*, *Pm53*, *Pm57*, and *Pm58*) [6,7,38,46,47,53,72,74,75,78,82], *Haynaldia villosa* (*H. villosa*, syn. *Dasyphyrum villosum*) (*Pm21* and *Pm55*)

[28,30], *Secale cereale* (*Pm7*, *Pm8*, *Pm17*, *Pm20*, and *Pm56*) [10,19,49,83], and *Thinopyrum* spp. (*Pm40*, *Pm43*, and *Pm51*) [45,64,69]. Within the 44 *Pm* genes derived from alien species or sparsely cultivated subspecies, 22 are assigned on the B genome, while only 14 are assigned on the A genome, and eight on the D genome (Table 2). The proportion of alien *Pm* genes within the whole *Pm* genes is 0.69 on B genome, while 0.33 on A genome and 0.47 on D genome; this large number and proportion of alien genes on the B genome may explain its high tolerance to the presence of alien chromatin. Most of the published alien *Pm* genes have not been successfully used in breeding in the past; however, several alien *Pm* genes have played an important role in Chinese wheat breeding.

### 2.1. Alien *Pm* genes widely used in Chinese wheat breeding

*Pm8*, one of the best-known and most widely used genes in wheat breeding, has played a major role in protecting wheat yield loss from powdery mildew infection. *Pm8* was transferred from the “Petkus” rye chromosome into hexaploid wheat in the early 1930s.

Cytological analysis showed that the rye chromosome arm 1RS was translocated to the wheat chromosome arm 1BL, resulting in the translocation chromosome T1BL.1RS [84]. In addition to powdery mildew resistance, the rye chromosome arm 1RS offers resistance to other diseases such as strip rust (caused by *Puccinia striiformis* f. sp. *tritici* [85,86]) and possesses desirable agronomic traits that increase wheat yield [87]. Hence, *Pm8*, as a valuable powdery mildew-resistance gene, was widely used in wheat-breeding programs and produced many wheat cultivars with resistance to powdery mildew; these include “Kavkaz,” “Apollo,” “Disponent,” and “CN10,” which have been widely grown around the world [10,88–92]. Although some newly emerged *Bgt* isolates overcame the resistance of *Pm8* in the 1990s [93], the use of *Pm8* in wheat-breeding programs continued, especially in the 21st century, because the wheat-rye 1BL.1RS translocated chromosome carrying *Pm8* has other excellent agronomic traits such as wide adaptability, high yield potential, and delayed leaf senescence [87,94]. Thus, *Pm8* has been effective against the powdery mildew pathogen for about 60 years and has played an important role in wheat resistance breeding around the world [95].

Another example of the successful use of an alien wheat powdery mildew-resistance gene is *Pm21*. In the early 1980s, *H. villosa* was identified as a potential source of powdery mildew resistance [96], and some alien addition lines and substitution lines developed from *H. villosa* showed resistance [97]. A resistance gene from *H. villosa*, designated as *Pm21*, was mapped on the wheat-*H. villosa* 6VS.6AL translocated chromosome [30]. The 6VS.6AL translocation lines carrying *Pm21* have been widely used as a parent in Chinese wheat-breeding programs because the other resistance genes have been overcome by newly emerged isolates, and because the use of *Pm21* has little adverse effect on other agronomic traits [98]. More than ten wheat cultivars carrying *Pm21* have been released in China since 2002; these include Yangmai 5, Yangmai 15, Yangmai 18, Neimai 8, and Neimai 9 [30,99,100], which have been grown on more than  $3.4 \times 10^6$  hm<sup>2</sup>, and this growth area is rapidly expanding, especially since 2007 [101]. Virulence testing revealed that *Pm21* shows a broad spectrum of resistance, and remains highly effective against most of the isolates of *Bgt* [102]; this indicates that the resistance of *Pm21* has lasted for more than 40 years. A few studies reported that new isolates of *Bgt* were virulent to *Pm21* [103,104]; however, two recent studies demonstrated that *Pm21* is still effective against 1082 *Bgt* isolates collected from eight major wheat-growing regions in China [105], and against 1402 *Bgt* isolates collected from 19 locations in Poland [106]. These results suggest that *Pm21* can still be used as a pivotal powdery mildew-resistance gene in wheat-breeding programs in the future.

## 2.2. The great potential of *Pm40* in wheat resistance breeding

In 2007, we identified two powdery mildew-resistant wheat lines, Yu24 and Yu25. These two wheat lines were derived from the cross between the wheat cultivar Chuanmai 107 and the octoploid *Tritigria* TAI7047, where the TAI7047 was derived from the cross between *T. aestivum* cv. Taiyuan 768/*Th. intermedium*//*T. aestivum* line 76(64). Genetic analysis suggested that the powdery mildew resistance was controlled by two pairs of Mendelian genes [107]. One of the genes, *Pm40*, was assigned to wheat chromosome arm 7BS by microsatellite markers [64].

*Pm40* is highly effective and durable against many *Bgt* isolates. The powdery mildew resistance of both Yu24 and Yu25 was originally observed over several consecutive years in fields at the Ya'an Agricultural Research Station of Sichuan Agricultural University in southwest China, where the climate is warm and humid, with a yearly average temperature of 15–17 °C and an average annual precipitation of 1520 mm [64]. These weather conditions favor epidemics of wheat diseases, and there exists a large variation in

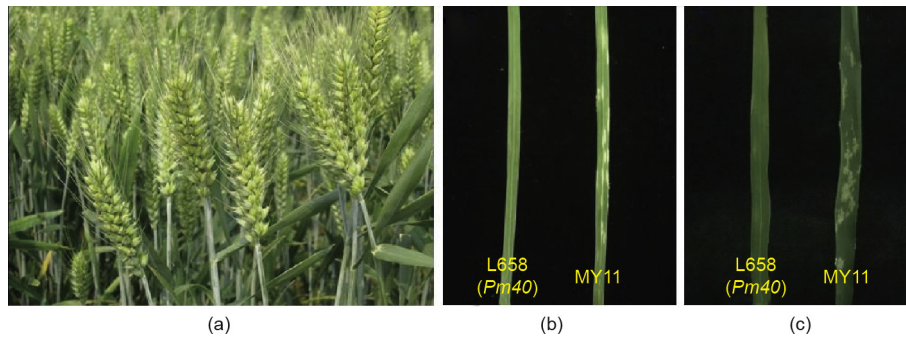
the virulence of *Bgt* [4]. These observations suggest that Yu24 and Yu25 may be resistant to various *Bgt* isolates. In fact, the resistance conferred by *Pm40* is still effective in fields located in the Chinese provinces of Henan, Shandong, Hebei, and Fujian [102]. A powdery mildew-resistance test in a greenhouse at the Institute of Crop Science, Chinese Academy of Agricultural Science, Beijing, demonstrated that the resistance in wheat line L658, conferred by *Pm40*, was resistant to all 28 of the *Bgt* isolates collected from various regions of China. This test displayed the board-spectrum and putatively durable character of *Pm40* (Table 3 [5] and Fig. 1), suggesting that *Pm40* holds great potential to be an important powdery mildew-resistance gene in wheat-breeding programs.

*Pm40* can be quickly integrated into commercial wheat cultivars. Alien chromosomal translocation has been a common and useful bridge for transferring genes from wild relatives to common wheat. However, the “linkage drag” that transfers other linked genes for undesirable traits together with the target gene from the alien translocation is a major drawback to the use of these resistance sources in breeding [108]. The original wheat lines Yu24 and Yu25, which were derived from the wild cross between common wheat and *Th. intermedium*, showed good genetic stability of powdery mildew resistance along with uniform agronomic traits in the field [107,109]. In addition, *Pm40* inherits as a normal Mendelian unit, and there are wheat-specific products in the resistant parent produced by polymerase chain reaction (PCR) amplifying. A wheat marker linked to *Pm40* and the closely linked DNA marker loci flanking *Pm40* show good agreement in loci order and flanking marker distances with the consensus genetic map [64]. No alien chromosomal segment is detected by *in situ* hybridization in any of the wheat lines carrying *Pm40* [4,110]. The good stability of the powdery mildew resistance conferred by *Pm40* ensures that

**Table 3**  
Infection types on wheat seedlings inoculated with *Bgt* isolates from different areas.

Isolate	Source	Wheat line (gene)		
		Coker 747 (Pm6)	Liangxing 99 (Pm52)	L658 (Pm40)
<i>Bgt68-2</i>	Beijing	0	0	0
<i>Bgt74-1</i>	Hebei	3	0	0
<i>Bgt87</i>	Beijing	3	0	0
<i>Bgt74-3</i>	Hebei	3	0	0
<i>Bgt86-3</i>	Jiangsu	2	0	0
<i>Bgt75-1</i>	Henan	2	0	0
<i>Bgt75-2</i>	Henan	3	0	0
<i>Bgt82-3</i>	Shandong	0	0	0
<i>Bgt88-3</i>	Shandong	3	0	0
<i>Bgt77-1</i>	Henan	3	0	0
<i>Bgt83-1</i>	Shandong	0	0	0
<i>Bgt81-2</i>	Shandong	4	0	0
<i>Bgt68-1</i>	Beijing	1	0	0
<i>Bgt69-1</i>	Hebei	3	0	0
<i>Bgt82-2</i>	Shandong	0	0	0
<i>Bgt78-3</i>	Henan	2	0	0
<i>Bgt79-2</i>	Shandong	3	3	0
<i>Bgt44-6</i>	Shandong	3	3	0
<i>Bgt76-3</i>	Henan	3	0	0
<i>Bgt78-2</i>	Henan	3	0	0
<i>Bgt68-3</i>	Beijing	1	0	0
<i>Bgt73-3</i>	Hebei	1	0	0
<i>Bgt72</i>	Hebei	2	0	0
<i>Bgt71-2</i>	Hebei	2	0	0
<i>Bgt44-4</i>	Shandong	0	3	0
<i>Bgt79-3</i>	Shandong	2	3	0
<i>Bgt75-3</i>	Henan	3	2	0
<i>Bgt28</i>	Sichuan	–	–	0

0: no visible symptoms; 1: hypersensitive necrotic flecks and small conidia with few conidiospores; 2: colonies with moderately developed conidia; 3: colonies with well-developed hyphae and abundant disconnected conidia; 4: well-developed hyphae and joined conidia [5].



**Fig. 1.** Powdery mildew responses on infected leaves of *Pm40*. (a) Wheat line L658 (*Pm40*) in the field; (b) infected leaves of the wheat lines L658 (resistant) and MY11 (susceptible) in the greenhouse 14 days after inoculation; (c) infected leaves of wheat lines L658 and MY11 in the field.

it can be quickly integrated into commercial wheat cultivars by molecular breeding methods.

The wheat lines containing *Pm40* usually have desirable agronomic traits and can easily be used in future Chinese wheat breeding. Breeders usually pay more attention to overall agronomic performance and to the effectiveness of resistance transferring than to where the resistance genes come from [4]. To accelerate the deployment of *Pm40* in wheat-breeding programs, we have developed some *Pm40* wheat lines, including L658 (PI 672537), L693 (PI 672538), L696 (PI 672539), and L699 (PI 672540). Many of these lines exhibit excellent agronomic traits such as good plant height, yield index, head weight, and thousand kernel weight. They also show resistance to multiple diseases [111]; for example, *YrL693* confers resistance to stripe rust [112], while *FhbL693a* and *FhbL693b* confer resistance to *Fusarium* head blight (caused by *Fusarium gramineum*) [110]. Molecular markers closely linked with *Pm40* have been identified. For example, we have identified two simple sequence repeats (SSRs) markers, *Xwmc335* and *Xgwm297*, and two sequence-tagged site-based expression-sequence tags (EST-STS), *BF291338* and *BE446359*. Both markers were less than one centimorgan to *Pm40* [4,64], which thus provides a useful tool for breeders to effectively transfer *Pm40* into commercial wheat cultivars using molecular marker-assistant selection. Finally, information on chlorophyll content, photosynthetic and chlorophyll fluorescence parameters, antioxidant activity, and gene expression after *Bgt* infection could be used as an additional reference for breeders in breeding practices [109]. Therefore, wheat lines containing *Pm40* are promising for the improvement of both yield and multiple disease resistance; in addition, the availability of the closely linked marker paves the way for breeders to achieve an effective transfer of *Pm40* into commercial wheat cultivars.

### 3. Deployment of powdery mildew-resistance wheat genes post-*Pm21* in China

Several new isolates of *Bgt* have been reported to be virulent to *Pm21* [103,104]. This indicates a forthcoming risk of powdery mildew epidemics in Chinese wheat production due to the loss of resistance of *Pm21*. Therefore, wheat breeders need to identify a replacement for *Pm21* for powdery mildew-resistance improvement. Among the published *Pm* genes, *Pm40* was derived from *Th. intermedium* and confers strong resistance to powdery mildew with a broad resistance spectrum [5]. In addition, wheat lines carrying *Pm40* usually have good yield traits, plant type, and resistance to other diseases such as stripe rust and *Fusarium* head blight [111]. Moreover, the stability of *Pm40* resistance and the molecular markers that are closely linked to *Pm40* [4,64] make it a good candidate for the replacement of *Pm21*. To effectively use *Pm40* in wheat breeding, we suggest that pyramiding of *Pm40* as the

major provider of resistance, along with the other *Pm* genes is an important strategy to control wheat powdery mildew.

### 4. Durability and effectiveness of alien resistance genes

A wheat-*Th. intermedium* introgression line was recently shown to have a broader spectrum of resistance against different *Bgt* isolates than the genes from wheat in popular resistant cultivars [3]. For stripe rust wheat resistance, several alien *Yr* genes, such as *Yr5* derived from *T. spelta album* [113], *Yr9* from rye [114], *Yr15* from *T. dicoccoides* [115], and *Yr26* from *T. turgidum* [116], have a broader spectrum of resistance against *Pst* than the *Yr* genes derived from common wheat. Although *Yr9* has lost its resistance to *Pst* races CYR29, CYR31, CYR32, and CYR33 [90], it has played an important role in the improvement of wheat resistance to stripe rust. *Yr26* is a major stripe rust-resistance gene that has been widely used in breeding and is still effective against current *Pst* races. Polymorphism at the loci that were derived from wide crossing contributes to parasite recognition, which will prevent loss of fitness due to disease; the more heterogeneous the host, the more incompatible it will be with pathogens [117]. Therefore, alien resistance genes usually provide a broader resistance spectrum and more potentially durable resistance than genes derived from crop itself. We assume that the larger variation in the DNA sequence of alien resistance genes, as compared with the genes from wheat, results in an increased resistance spectrum and in a delayed process of compatible reaction between the host and pathogens in alien genes. This hypothesis will provide new insight into selecting powdery mildew-resistance genes to be deployed in breeding programs in the future.

### 5. Conclusion

With its broad resistance spectrum, *Pm40*, as one of the important *Pm* genes derived from alien species or sporadically grown subspecies, could play a key role in the improvement of Chinese wheat resistance to powdery mildew. The potential of *Pm40* has become even more important since the powdery mildew resistance conferred by *Pm21* has been overcome by newly emerged *Bgt* isolates. In addition, further elucidation of the resistance mechanism of *Pm40* would accelerate its application in wheat-breeding programs.

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### Compliance with ethics guidelines

Shengwen Tang, Yuting Hu, Shengfu Zhong, and Peigao Luo declare that they have no conflict of interest or financial conflicts to disclose.

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