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抗白粉病基因 *Pm40* 在我国“后 *Pm21* 时代”小麦育种中的重要作用

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摘要

由小麦白粉菌 [*Blumeria graminis* f. sp. *tritici*（*Bgt*）] 引起的小麦白粉病是一种重要的小麦叶部病害，对小麦的产量产生很大的影响。20 世纪 80 年代，通过簇毛麦（*Heuchera villosa*）的 6VS 染色体与小麦 6AL 染色体易位将抗白粉病基因 *Pm21* 转移到普通小麦中。最近，在一些地方发现了对 *Pm21* 有毒的 *Bgt*，虽然这些菌株的病理学特性还有待研究，但这一现象提醒小麦育种者应注意应用 *Pm21* 的风险。来源于普通小麦与中间偃麦草（*Thinopyrum intermedium*）杂种后代的抗白粉病基因 *Pm40*，被定位在小麦 7BS 染色体上，对 *Bgt* 具有广谱和持久的抗性。通过细胞学研究，并未在 *Pm40* 的载体品种中发现大片段外缘染色体。过去几年的研究发现，*Pm40* 的载体品种具有优良的农艺性状。因此，我们相信在未来的育种工程中，*Pm40* 将会在 *Pm21* 的抗性被克服之后起巨大的作用。另外，*Pm21* 和 *Pm40* 都来源于外缘物种，这暗示着外源基因的抗性可能比小麦本身的基因更为持久和有效。

1. 引言

由小麦白粉菌[*Blumeria graminis* f. sp. *tritici*（*Bgt*）]引起的小麦白粉病是世界范围内的一种重要真菌性病害，严重影响小麦[*Triticum aestivum* L.（*T. aestivum* L.）]的产量。自20世纪70年代以来，小麦白粉病在我国的大多数冬小麦生产地区发生，对小麦的产量及品质造成了严重的损失[1]。虽然过去小麦白粉病在中国西南地区是次于条锈病[由条锈菌*Puccinia striiformis* f. sp. *tritici*（*Pst*）引起]的第二大病害，但由于半矮秆品种的推广、水肥条件的改善和氮肥使用量的增加，现在白粉病的危害程度已经超过了条锈病，成为最具破坏性的小麦叶部病害[2–4]。

化学防治和合理的栽培措施虽能在一定范围内有效地控制白粉病的发生，但培育新的抗病品种不仅可以降低杀菌剂施用的生产成本，还能减少环境污染，是控制白粉病的最佳措施[5]。抗白粉病（*Pm*）基因是培育抗病小麦品种的前提，因此，小麦育种者一直致力于发掘新的抗白粉病基因来提高小麦对白粉病的抗性。目前，已在小麦染色体的54个基因座（表1）[1,4,6–10,12–78]发现了91个*Pm*基因（其中*Pm18* = *Pm1c*，*Pm22* = *Pm1e*，*Pm23* = *Pm4c*，*Pm17* = *Pm8*，*Pm31* = *Pm21*，*Pm48* =

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Pm46）[6–12]。这些基因分布在小麦除了3D和4D染色体之外的所有染色体上。在54个*Pm*基因座中，有27个（50.0%）位于B染色体组，只有13个（24.1%）位于D染色体组（表2）。在这些抗白粉病基因中，有42个基因（46.2%）位于A染色体组，只有17个基因（18.7%）位于D染色体组。在A、B、D 3个小麦染色体组上，平均每个*Pm*基因座的等位基因数目分别为3.00、1.19和1.31。A染色体组平均每个*Pm*基因座的等位基因数目高于B染色体组和D染色体组。此外，从表2还可以看出，从外缘物种转移到小麦A、B染色体组的外源*Pm*基因通常会表现出广谱性和持久性，如*Pm21*和*Pm40*。

2. 外源 *Pm* 基因对提高小麦白粉病抗性的作用

野生近缘种的抗病基因对多种病原菌具有持久抗性，将其转移到小麦中，是现代育种体系的重要组成部分[79]。在正式命名的54个*Pm*基因中，有位于37个基因座的44个基因来源于野生近缘种，包括野生一

表1 小麦白粉病抗性基因及其染色体分布

Chromosome	Locus	Genes from *T. Aestivum*	Genes from alien species
1A	*Pm3*, *Pm25*	*Pm3a* [13], *Pm3b* [13], *Pm3c* [14], *Pm3d* [15], *Pm3e* [15], *Pm3f* [15], *Pm3g* [16], *Pm3h* [16], *Pm3i* [16], *Pm3j* [16], *Pm3l* [17], *Pm3m* [18], *Pm3n* [18], *Pm3o* [18], *Pm3p* [18], *Pm3q* [18], *Pm3r* [18]	*Pm3k* (*T. turgidum dicoccon*) [17], (*Secale cereale* (*S. cereale*)) [19], *Pm25* (*T. boeoticum*) [20]
2A	*Pm4*, *Pm50*	*Pm4c* (*Pm23*) [9], *Pm50* [21]	*Pm4a* (*T. dicoccum*) [14,22], *Pm4b* (*T. carthlicum*) [23,24], *Pm4d* (*T. monococcum*) [25]
3A	*Pm44*	*Pm44* [26]	
4A	*Pm16*		*Pm16* (*T. dicoccoides*) [27]
5A	*Pm55*		*Pm55* (5AL/5DL) (*Dasypyrim villosa*) [28]
6A	*Pm21, Pm56*		*Pm21* (*Pm31*) (*Haynaldia villosa*) [29,30], *Pm56* (*S. cereale*) [124]
7A	*Pm1*, *Pm9*, *Pm37*, *Pm59, Pm60*	*Pm1a* [31,32], *Pm1c* (*Pm18*) [7,33], *Pm1e* (*Pm22*) [8], *Pm9* [34], *Pm59* [125]	*Pm1b* (*T. monococcum*) [7], *Pm1d* (*Aegilops speltoides* (*Ae speltoides*)) [7], *Pm37* (*T. timopheevi*) [35], *Pm60* (*T. urartu*) [123]
1B	*Pm8*, *Pm28*, *Pm32*, *Pm39*	*Pm28* [36], *Pm39* [37]	*Pm8* (*Pm17*) (*Secale cereale* (*S. cereale*)) [10], *Pm32* (*Ae.gilops speltoides*) [38]
2B	*Pm6*, *Pm26*, *Pm33*, *Pm42*, *Pm49*, *Pm51*, *Pm52*, *Pm57*	*Pm52* [1]	*Pm6* (*T. timopheevi*) [39,40], *Pm26* (*T. dicoccoides*) [41], *Pm33* (*T. carthlicum*) [42], *Pm42* (*T. turgidum dicoccon*) [43], *Pm49* (*T. turgidum dicoccon*) [44], *Pm51* (*Th. ponticum*) [45], *Pm57* (*Ae. searsii*) [46]
3B	*Pm13*, *Pm41*		*Pm13* (*Ae. longissima*) [47], *Pm41* (*T. turgidum dicoccon*) [48]
4B	*Pm7*		*Pm7* (*S. cereale*) [49,50]
5B	*Pm30*, *Pm36*, *Pm53*		*Pm30* (*T. dicoccoides*) [51], *Pm36* (*T. turgidum dicoccon*) [52], *Pm53* (*Ae. speltoides*) [53]
6B	*Pm11*, *Pm12*, *Pm14*, *Pm20*, *Pm27*, *Pm54*	*Pm11* [54], *Pm14* [55], *Pm54* [56]	*Pm12* (*Ae. speltoides*) [57], *Pm20* (*S. cereale*) [49], *Pm27* (*T. timopheevii*) [58],
7B	*Pm5*, *Pm40*, *Pm47*	*Pm5c* [59], *Pm5d* [59,60], *Pm5e* [61], *Pm47* [62]	*Pm5a* (*T. dicoccum*) [63], *Pm5b* (*T. dicoccum*) [59], *Pm40* (*Thinopyrum intermedium* (*Th. intermedium*)) [4,64]
1D	*Pm10*, *Pm24*	*Pm10* [65], *Pm24a* [66,67], *Pm24b* [68]	
2D	*Pm43*, *Pm58*		*Pm43* (*Th. intermedium*) [69], *Pm58* (*Ae. tauschii*) [6]
5D	*Pm2*, *Pm34*, *Pm35*, *Pm46*	*Pm2c* [70,71], *Pm46* (*Pm48*) [12]	*Pm2a* (*Ae. tauschii*) [72,73], *Pm2b* (*Agropyron cristatum* (*A. cristatum*)) [70], *Pm34* (*Ae. tauschii*) [74], *Pm35* (*Ae. tauschii*) [75]
6D	*Pm45*	*Pm45* [76]	
7D	*Pm15*, *Pm19*, *Pm29*, *Pm38*	*Pm15* [55], *Pm38* [77]	*Pm19* (*Ae. squarrosa*) [72,73], *Pm29* (*Ae. ovate*) [78]

表2 正式命名的抗白粉病基因在小麦A、B和D基因组上的分布

Genome	Number of loci	Number of *Pm* 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

粒小麦（*Pm25*）[20]、栽培一粒小麦（*Pm1b*和*Pm4d*）[7,25]、野生二粒小麦 [27,29,41,51]、栽培二粒小麦（*Pm4a*、*Pm5a*和*Pm5b*）[59,63,80]、波斯小麦（*Pm4b*和*Pm33*）[23]、野生二粒小麦 [17,43,44,48,52]、提莫菲维小麦（*Pm6*、*Pm27*和*Pm37*）[35,39,58]、乌拉尔图小麦（*Pm60*）[81]、冰草属（*Pm2b*）[70]、山羊草属（*Pm1d*、*Pm2a*、*Pm12*、*Pm13*、*Pm19*、*Pm29*、*Pm32*、*Pm34*、*Pm35*、*Pm53*、*Pm57*和*Pm58*）[6,7,38,46,47,53,72,74,75,78,82]、簇毛麦属（*Pm21*和*Pm55*）[28,30]、黑麦属（*Pm7*、*Pm8*、*Pm17*、*Pm20*和*Pm56*）[10,19,49,83]和偃麦草属（*Pm40*、*Pm43*和*Pm51*）[45,64,69]。在这44个外源*Pm*基因中，有22个位于B染色体组，14个位于A染色体组，8个位于D染色体组（表2）。外源*Pm*基因的个数在B染色体组中占比为0.69，然而在A、D染色体组中占比分别只有0.33和0.47。B染色体组中外源*Pm*基因的数量和占比可能说明它对外缘染色体有较高的耐受性。在过去的育种实践中，大多数外源*Pm*基因并没有被成功运用于生产，然而，少数应有的基因在我国小麦育种史上起着至关重要的作用。

2.1. 外源 *Pm* 基因在中国小麦育种中的广泛应用

*Pm8*是应用范围最广、最为人熟知的白粉病抗性基因之一，在防止小麦白粉病造成的产量损失方面发挥了重要作用。20世纪30年代早期，*Pm8*从黑麦（Petkus）染色体转移到六倍体小麦染色体上，细胞学分析表明，黑麦1RS染色体与小麦1BL染色体发生易位，产生T1BL 1RS染色体易位系[84]。除了抗白粉病之外，黑麦1RS染色体上还存在抗小麦条锈病等其他病害的基因[85,86]，而且具有良好的农艺性状[87]。因此，*Pm8*作为一种有价值的抗白粉病基因，在小麦育种中得到广泛的应用。*Pm8*的载体品种在世界范围内被大面积种植，如“Kavkaz”“Apollo”“Disponent”“CN10”等[10,88–92]。虽然在20世纪90年代，一些新出现的*Bgt*克服了*Pm8*的抗性[93]，但在21世纪的小麦育种工作中，*Pm8*仍然被广泛地使用，这是因为含有*Pm8*的小麦-黑麦T1BL 1RS易位系具有适应性广、产量高、能延迟叶片衰老等优良性状[87,94]。因此，*Pm8*有效抵御小麦白粉病约60年，在全球小麦抗性育种中发挥了重要作用[95]。

另一个外源抗白粉病基因成功应用的例子是*Pm21*。在20世纪80年代早期，簇毛麦被认为是白粉病一个的潜在抗源[96]，一些来源于簇毛麦的外缘附加系对小麦白粉病表现出良好的抗性[97]。来源于簇毛麦的小麦抗白粉病基因*Pm21*位于簇毛麦-小麦的T6VS 6AL易位染色体上[30]。由于其他生产上应用的抗病基因的抗性大多已被新出现的有毒菌株所克服，所以携带*Pm21*的T6VS 6AL易位系作为亲本在我国小麦育种中得到了广泛的应用，并且其载体品种并没有携带不良农艺性状[98]。自2002年以来，我国利用*Pm21*基因培育了10多个小麦品种，如扬麦5号、扬麦15、扬麦18、内麦8号、内麦9号等[30,99,100]，这些含有*Pm21*的品种种植面积超过3.4×10^6 hm^2，特别是自2007年以来，种植面积迅速扩大[101]。抗性鉴定结果表明，*Pm21*具有广谱抗性，对大多数*Bgt*具有很强的抗性[102]，这说明*Pm21*的抗性至今已经持续了40多年。尽管有少数研究发现了对*Pm21*具有毒性的*Bgt* [103,104]，但最近的两项研究表明，*Pm21*对中国8个主要小麦产区收集的1082个*Bgt*仍然有效[105]，并对波兰19个地区收集的1402个白粉菌菌株有效[106]。所以，目前*Pm21*仍可作为小麦育种中重要的抗白粉病基因。

2.2. 小麦抗白粉病基因 *Pm40* 在小麦抗病育种中的巨大潜力

2007年，我们发现了两个对白粉病具有抗性的小麦品种Yu24和Yu25，这两个小麦品种来源于普通小麦川麦107和八倍体小偃麦TAI7047的杂种后代，而TAI7047则是来源于普通小麦太原768/中间偃麦草//普通小麦76（64）的杂种后代。遗传分析表明，Yu24和Yu25的白粉病抗性受两对基因控制[107]。利用SSR标记将其中一个抗病基因*Pm40*定位在小麦7BS染色体上[64]。

*Pm40*对白粉病的抗性表现出既高效又持久的特点。雅安气候温暖潮湿，年平均气温为15~17 ℃，年平均降水量为1520 mm [64]，这些气候条件有利于小麦疾病的流行，而且存在着很多不同有毒*Bgt*的变异[4]。所以我们在四川农业大学雅安实验基地对Yu24和Yu25进行了

连续多年的抗性鉴定，结果表明，这两个材料对不同*Bgt*均具有抗性。而且，在河南、山东、河北、福建等地，*Pm40*也表现出了很强的抗性[102]。中国农业科学院在温室中进行的白粉病抗性鉴定结果表明，含有*Pm40*的小麦品系L658对来自中国不同地区的28个*Bgt*都具有抗性，这一结果也充分地肯定了*Pm40*的广谱性和持久性（表3[5]、图1），表明*Pm40*在小麦育种工作中是一个非常具有潜力的重要抗白粉病基因。

*Pm40*基因可以迅速地整合到小麦推广品种中。染色体易位是将基因从野生亲本转移到普通小麦的一种常用的有效手段，但这种遗传方式有可能会将其他不良性状相关的基因与所需要的目的基因连锁，这是在育种中使用这些染色体易位系的主要障碍之一[108]。Yu24和Yu25来源于普通小麦与中间偃麦草的杂种后代，对白粉病的抗性具有良好的遗传稳定性，且田间农艺性状表现一致[107,109]。此外，*Pm40*作为正常的孟德尔遗传单元，抗病亲本能通过聚合酶链反应（PCR）扩增出特异性产物，与*Pm40*连锁的小麦标记，在遗传图谱上的遗传距离与顺序均表现出良好的一致性[64]。在所有*Pm40*的载体品种（系）中，通过原位杂交均未检测到外缘染色体片段[4,110]。所以我们可以通过分子育种的方法将*Pm40*所表现出的白粉病抗性的良好稳定性，迅速整合到小麦推广品种中。

含有*Pm40*的小麦品种（系）通常具有良好的农艺性状，很容易用于小麦育种。比起抗病基因的来源，育种者通常更关注小麦的农艺性状以及抗性转移的有效性[4]。为了加快*Pm40*在小麦育种中的应用，我们培育了一些*Pm40*的小麦载体品系，包括L658（PI 672537）、L693（PI 672538）、L696（PI 672539） 和L699（PI 672540）。其中许多品系都具有优良的农艺性状，如株高、产量指数、穗重和千粒重。同时，它们还具有小麦其他重要病害的抗病基因[111]，如抗条锈病基因*YrL693*[112]以及抗赤霉病基因*FhbL693a*和*FhbL693b* [110]。另外，我们还发现了两个与*Pm40*紧密连锁的SSR标记（*Xwmc335*和*Xgwm297*），以及两个EST-STS（*BF291338*和*BE446359*）标记，两种分子标记与*Pm40*基因的遗传距离均小于1 cM[4,64]，这为育种者利用分子标记辅助育种技术有效地将*Pm40*导入小麦品种提供了一个有效的工具。最后，叶绿素含量、光合作用、叶绿素荧光参数、抗氧化活性和*Bgt*侵染后的各种基因的表达量等信息都可以为育种实践提供参考[109]。因此，含*Pm40*的小麦品种（系）具有提高产量和抗多种病害的潜力。此外，与基因紧密连锁的标记为育种者将*Pm40*有效地转移到小麦推广品种奠定了基础。

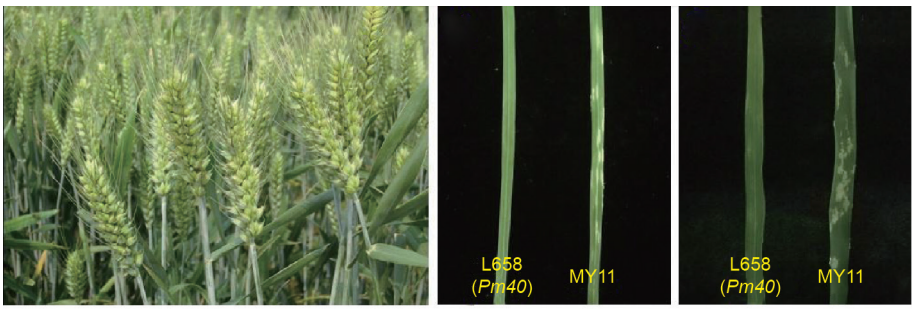
3. 继 *Pm21* 之后小麦白粉病抗性基因在我国的应用

有少数研究称发现了对*Pm21*具有毒性的新的*Bgt*[103,104]。这表明，一旦*Pm21*失去抗性，我国小麦生产随时可能会面临白粉病大爆发所带来的危机。因此，小麦育种者需要找到一个能替代*Pm21*的基因来提

表3 不同小麦幼苗对来源于不同地区的*Bgt*的反应

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



(a) (b) (c)

图1. 含有*Pm40*小麦材料的叶片反应。(a) L658(*Pm40*)的田间生长情况;(b) 温室内L658(抗病)和MY11(感病)接种后14 d后的反应;(c) L658(抗病)和MY11(感病)田间反应。

高小麦对于白粉病的抗病能力。在已知的抗白粉病基因中，*Pm40*来源于中间偃麦草，具有较强的白粉病抗性[5]。而且，*Pm40*的小麦载体品种（系）具有良好的农艺性状，如株高、产量以及对条锈病、赤霉病等小麦其他主要病害的抗性[111]。此外，*Pm40*抗性的稳定性和与*Pm40*紧密连锁的分子标记使之可能成为替代*Pm21*的优秀候选基因[4,64]。为了使*Pm40*在小麦育种中更好地发挥作用，我们认为将*Pm40*作为主要的抗性供体，并整合联用其他抗白粉病基因是控制小麦白粉病的重要策略。

4. 外源抗病基因的有效性和持久性

比起来自于小麦本身的基因，小麦与中间偃麦草的杂种后代对*Bgt*具有广谱抗性[3]。对小麦条锈病而言，一些外缘抗条锈病基因比来源于普通小麦的抗条锈病基因的抗谱更广，如来源于斯卑尔脱小麦的*Yr5* [113]、黑麦的*Yr9* [114]、野生二粒小麦的*Yr15* [115]和圆锥小麦的*Yr26* [116]。虽然*Yr9*已经丧失了对CYR29、CYR31、CYR32、CYR33等条锈菌的抗性[90]，但是*Yr9*对于提高小麦对条锈病的抗性的确起到了重要的作用。*Yr26*是目前在育种中广泛应用的抗条锈病基因，对当前流行的条锈菌生理小种仍有效。通过远缘杂交产生的多态性基因座有助于对病原菌的识别，这种识别过程将保护作物不受到外界病害的侵害，宿主产生的基因座多态性越高，与病原体的不亲和程度就越高[117]。因此，与来自作物本身的基因相比，外源抗性基因通常抗谱更广，抗性更持久。所以我们认为，与来源于小麦自身的基因相比，外源抗病基因的DNA序列变异更大，可使外源基因的宿主和病原体之间的亲合反应发生延迟，从而导致外源基因比小麦本身基因的抗性更强。这一假设可能为今后育种工作中选择抗白粉病基因提供新的见解。

5. 结论

具有广谱抗性的*Pm40*作为一个来源于外缘植物的重要*Pm*基因，将在我国对小麦白粉病的防治中发挥关键作用。特别是当*Pm21*的抗性被新的*Bgt*克服之后，*Pm40*可能将更加重要。此外，进一步阐明*Pm40*的抗病机制，将加速其在小麦育种中的应用。

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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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