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小麦慢白粉病 QTL 对条锈病和叶锈病的兼抗性

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摘 要: 聚合兼抗白粉病、条锈病和叶锈病的慢病性基因, 是培育持久多抗小麦品种的重要措施。百农 64 和鲁麦 21 均为慢白粉病品种, 分别含有 4 个和 3 个慢白粉病抗性 QTL。将百农 64 与鲁麦 21 杂交, 获得 21 个聚合 2~5 个慢白粉病抗性 QTL 的 F_6 株系, 于 2012—2013 年度分别在四川郫县和甘肃天水进行条锈病田间抗性鉴定,在河北保定和河南周口进行叶锈病田间抗性鉴定。分析 21 个株系条锈和叶锈病的最大严重度和病程曲线下面积, 检测单个 QTL 和 QTL 聚合体对条锈病和叶锈病的抗性效应。结果表明, *QPm.caas-4DL*、*QPm.caas-6BS* 和 *QPm.caas-2BL* 对条锈病均有显著的抗性, 分别解释表型变异的 16.9%、14.1%和 17.3%; *QPm.caas-4DL* 对叶锈病也有显著抗性, 可解释表型变异的 35.3%; *QPm.caas-1A*/*QPm.caas-4DL*/ *QPm.caas-2DL*/*QPm.caas-2BS*/*QPm.caas-2BL* 和 *QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2BS*/*QPm.caas-2BL* 聚合体对条锈病和叶锈病的抗性显著高于两亲本, 它们均含有来自百农 64 的 *QPm.caas-4DL* 以及来自鲁麦 21 的 *QPm.caas-2BL* 和 *QPm.caas-2BS*, 表明这些 QTL 具有明显的兼抗性效应。在小麦抗病育种中, 聚合慢病性 QTL 越多, 慢病性越强, 聚合 4~5 个慢病性 QTL 时, 株系可达到高抗甚至接近免疫的水平, 是选育持久抗性小麦品种的重要手段。

关键词: 普通小麦; 慢病性; 持久抗性; 基因聚合; QTL

Resistance of Slow Mildewing Genes to Stripe Rust and Leaf Rust in Common Wheat

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Abstract: Pyramiding quantitative trait loci (QTLs) is an effective method to improve resistance to powdery mildew, stripe rust, and leaf rust in common wheat. We have developed 21 lines (F_6) carrying 2-5 slow mildewing QTLs by crossing slow powdery mildew cultivars Bainong 64 and Lumai 21 possessing four and three slow mildewing QTLs, respectively. These F_6 lines were evaluated in the field in Pianxian, Sichuan and Tianshui, Gansu for stripe rust resistance and in Baoding, Hebei and Zhoukou, Henan for leaf rust resistance during the 2012-2013 cropping season. According to the maximum disease severities (MDS) and the area under the disease progress curve (AUDPC), QTLs *QPm.caas-4DL*, *QPm.caas-6BS* and *QPm.caas-2BL* were highly resistant to stripe rust ($P < 0.01$), which explained 16.9%, 14.1%, and 17.3% of phenotypic variance, respectively. Locus *QPm.caas-4DL* also showed high resistance to leaf rust ($P < 0.01$) with phenotypic contribution of 35.3%. Lines that pyramided five (*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2DL*/*QPm.caas-2BS*/*QPm.caas-2BL*) and four (*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2BS*/*QPm.caas-2BL*) QTLs exhibited higher resistance to both stripe and leaf rust compared with their parents. This result

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indicates that the combination of *QPm.caas-4DL* (from Bainong 64), *QPm.caas-2BS* and *QPm.caas-2BL* (Lumai 21) has a marked effect on improving adult resistance to powdery mildew, stripe rust and leaf rust, and the more QTLs are pyramided, the stronger slow disease resistance can be achieved. In breeding practice, the combination of 4-5 slow mildewing or rusting QTLs can result in durable resistance to multiple diseases.

Keywords: *Triticum aestivum* L.; Slow mildewing and slow rusting resistance; Durable resistance; Gene pyramiding; QTL

小麦白粉病、条锈病和叶锈病是全球性重要病害，分别由小麦白粉菌(*Blumeria graminis* f. sp. *tritici*)、小麦条锈菌(*Puccinia striiformis* f. sp. *tritici*)和小麦叶锈菌(*P. recondita* f. sp. *tritici*)引起，具有发生频率高、流行范围广和暴发性强的特点，可致3.0%~49.0%的产量损失[1-3]。长期以来，利用寄主抗性防治这些病害取得了显著成效[4]。

寄主抗性分为垂直抗性和水平抗性。垂直抗性又称为生理小种专化性抗性、苗期抗性、全生育期抗性或主效基因抗性，是由 1 个或少数几个主效基因控制，对特定病原菌生理小种表现出高抗或免疫，具有病原菌生理小种专化性，常因病原菌生理小种变异而丧失抗性；水平抗性亦称慢病性、成株抗性或非小种专化抗性，由多个微效基因控制，对病原菌无小种专化性或专化性弱，苗期表现为感病，成株期表现为中抗或高抗，且抗性持久[5-6]。慢病性由多个微效基因的加性效应控制，基因聚合是获得慢病性、选育兼抗多种病害品种的重要方式。Singh 等[7]发现，聚合 4~5 个微效慢病基因的小麦材料对条锈和叶锈病呈高抗至免疫。意大利小麦品种 Strampelli 和 Libellula 及我国农家种平原 50 至今仍然高抗条锈病。抗性遗传分析表明，Strampelli 和 Libellula 含有 *Yr18/Lr34/Pm38/Sr57* 和 2~4 个其他慢病基因[8]；平原 50 含有 3 个慢条锈基因和 3 个慢白粉基因[9]。*Yr18/Lr34/Pm38/Sr57* 对小麦条锈病、叶锈病、白粉病和秆锈病均具有抗性[10-11]。

随着QTL定位和分子标记研究工作的不断深入，育种家可以利用分子标记聚合抗病 QTL，培育持久抗性品种[7,12-13]。从 20 世纪 70 年代开始，国际玉米小麦改良中心(CIMMYT)选育出一批抗性持久且兼抗多种病害的慢病性品种，例如 Amadina、Chapio、Cook、Kukuna、Parula、Pavon 76、Sonoita 81、Tonichi 81 和 Tukuru，均含有 *Yr18/Lr34/Pm38/Sr57* 或 *Yr29/Lr46/Pm39/Sr58* 位点及 2~3 个微效基因[14-15]。因此，聚合慢病性基因是获得兼抗多种病害的持久抗性小麦品种的重要手段。

虽然小麦抗病性 QTL 定位研究很多，但是由于不同遗传背景下的 QTL 聚合到同一遗传背景存在诸多困难[16]，不同来源的 QTL 可能存在互作，QTL 聚合育种实践的报道很少。Miedaner 等[17]将 3 个来源不同的赤霉病抗性 QTL 聚合到同一种质，发现单个 QTL 均可降低赤霉病发病率和脱氧雪腐镰刀菌烯醇(DON)含量，但 3A 上的一个 QTL 单独存在或与 3B 和 5A 上 QTL 聚合时对赤霉病没有显著遗传效应。Lu 等[18]将 5A 上的 QTL 与 *Fhb1* 聚合在一起，发现可以降低矮秆基因 *Rht-D1b* 对赤霉病引起的效应。可见，QTL 聚合体遗传效应分析具有重要的应用价值。

百农 64 和鲁麦 21 均具有优良的农艺性状，分别在 20 世纪 90 年代和 21 世纪初为我国黄淮麦区主推品种，其苗期对白粉菌[19]、条锈菌和叶锈菌[20]流行小种均感病，但田间成株期表现抗病，具有典型的慢病性特征。在百农 64 中检测到 4 个慢白粉病抗性 QTL (*QPm.caas-1A*、*QPm.caas-4DL*、*QPm.caas-6BS* 和 *QPm.caas-7A*) [21]，在鲁麦 21 中检测到 3 个慢白粉病抗性 QTL (*QPm.caas-2BS*、*QPm.caas-2BL* 和 *QPm.caas-2DL*) [22]。Bai 等[23]采用杂交和改良系谱法，对百农 64 和鲁麦 21 所含慢白粉病抗性 QTL 进行聚合，创制了 21 个 F_6 聚合株系，并对这些材料的白粉病抗性进行了分析。在此基础上，本研究将分析这 21 个聚合不同慢白粉病基因的株系对条锈病和叶锈病的遗传效应，明确这些慢白粉病抗性 QTL 及 QTL 聚合体对条锈病和叶锈病的抗性，发掘高抗条锈、叶锈和白粉病的慢病性材料和 QTL 组合，为选育兼抗多种病害的持久抗性小麦品种提供材料和方法。

1 材料与方法

1.1 聚合株系基因型及其分子标记

百农 64 与鲁麦 21 杂交，采用改良系谱法，根据田间白粉病抗性和综合农艺性状选择，在早代淘汰白粉病严重度高的株系，选择低严重度株系继续种植，经过连续多代鉴定和选择，获得 21 个 F_6 抗病株系(编号：BFB5~BFB25)[23]；利用 16 个分子标记[21-22]进行检测，明确这些株系携带 2~5 个慢白粉病 QTL。这些慢白粉病 QTL 中，*QPm.caas-1A* 的连锁标记为

Xbarc148 和 *Xwmc550*, *QPm.caas-4DL* 的连锁标记为 *Xgwm165*、*Xcfd23* 和 *Xwmc331*, *QPm.caas-6BS* 的连锁标记为 *Xbarc79* 和 *Xgwm518*, *QPm.caas-7A* 的连锁标记为 *Xbarc127* 和 *Xbarc174*, *QPm.caas-2BS* 的连锁为 *Xbarc98* 和 *Xbarc1147*, *QPm.caas2BL* 的连锁标记为 *Xbarc1139* 和 *Xgwm47*, *QPm.caas-2DL* 的连锁标记为 *Xbarc18*、*Xgwm539* 和 *Xcfd233*。

1.2　田间设计

将 21 个 F_6 聚合基因株系及其亲本于 2012—2013 年度种植于四川郫县(30°05′N, 102°54′E)和甘肃天水(34°05′N′, 104°35′E)进行条锈病抗性鉴定; 在河北保定(113°40′N, 38°10′E)和河南周口(114°38′N, 33°37′E)进行叶锈病抗性鉴定。采用完全随机区组设计, 3 次重复, 单行区, 行长 1.5 m, 行距 0.25 m, 每行种植 50 粒。在郫县和天水点, 每 10 行种植 1 行高感条锈病品种对照辉县红, 小区周围种植高感品种作为诱发行; 在保定和周口, 每 10 行种植 1 行高感叶锈病对照郑州 5389。以保证充分接种, 实际观察所有对照均发病完全。

1.3　抗病性评价

接种后 6 周左右, 当对照品种充分发病时开始调查发病严重度, 记录旗叶和倒二叶上条锈菌或叶锈菌孢子堆面积占总叶片面积的百分数。每隔 7 d 调查一次, 共调查 2~3 次, 直到叶片上孢子堆不再增加为止。

用最大严重度(maximum disease severity, MDS)和病程曲线下面积(area under the disease progress curve, AUDPC)作为抗病性评价指标。

$$\mathrm{AUDPC} = \sum \frac{x_i + x_{i+1}}{2}(t_{i+1} - t_i)$$

式中 x_i 表示第 i 次调查的严重度, t_i 表示第 i 次调查距接种后的天数 [24]。用 SAS 9.2 软件进行统计分析和显著性比较。

2　结果与分析

2.1　21 个基因聚合株系条锈病和叶锈病抗性鉴定

MDS 和 AUDPC 在株系间和环境间的差异均达极显著水平($P<0.01$)。百农 64 和鲁麦 21 在郫县和天水两个环境下条锈病平均 MDS 分别为 36.8%和 50.0%, 平均 AUDPC 分别为 210.6 和 290.5; 12 个聚合基因株系的条锈病平均 MDS 均低于百农 64 和鲁麦 21。其中, 株系 BFB14 在两个环境下的条锈病平均 MDS 值(16.2%)和平均 AUDPC 值(92.1)最低; 在保定和周口的叶锈病平均 MDS 分别为 15.8%和 35.0%, 平均 AUDPC 分别为 91.6 和 212.3。其他 11 个株系的叶锈病平均 MDS 低于百农 64 和鲁麦 21。株系 BFB9 在两个环境下叶锈病的平均 MDS (3.6%)和平均 AUDPC (18.9)最低(表 1)。

2.2　慢白粉病 QTL 对条锈和叶锈病的抗性效应与互作分析

QPm.caas-4DL、*QPm.caas-2BS* 和 *QPm.caas-2BL* 对条锈病具有显著的抗性遗传效应($P<0.01$), 分别解释条锈病平均表型变异的 16.9%、14.1%和 17.3%, *QPm.caas-6BS* 可解释 1.8%的表型变异。*QPm.caas-2BS* 和 *QPm.caas-2BL* 之间存在互作, 但效应较低, 环境与 QTL 间也存在互作。*QPm.caas-4DL* 对叶锈病也具有显著抗性, 可解释表型变异的 35.3%, 而 *QPm.caas-6BS* 可解释 8.3%的表型变异(表 2)。

2.3　慢白粉病 QTL 聚合体对条锈和叶锈病的抗性效应

百农 64 和鲁麦 21 以及 21 个慢病性 QTL 聚合株系中共有 11 种 QTL 组合(表 3)。*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2DL*/*QPm.caas-2BS*/*QPm.caas-2BL* 和 *QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2BS*/*QPm.caas-2BL* 聚合体的条锈病 MDS 及 AUDPC 值最低, 远低于两亲本及其他 7 种 QTL 聚合体, 且差异显著($P<0.05$), 对条锈和叶锈病有较好的抗性。*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-7A* 组合的条锈病 MDS 和 AUDPC 最高, 与鲁麦 21 差异不显著, 但显著高于百农 64 及其他 8 种 QTL 聚合体($P<0.05$), 21 个聚合株系中其余 6 种 QTL 聚合体抗性与百农 64 差异不显著。

QPm.caas-1A/*QPm.caas-4DL*/*QPm.caas-2DL*/*QPm.caas-2BS*/*QPm.caas-2BL*、*QPm.caas-1A*/*QPm.caas-4DL*/ *QPm.caas-2BS*/*QPm.caas-2BL* 和 *QPm.caas-1A*/*QPm.Caas-4DL*/*QPm.caas-2BS* 组合的叶锈病 MDS 及 AUDPC 值较低, 显著低于双亲及其他 6 种 QTL 聚合体, 且差异显著($P<0.05$), 对叶锈病有较好抗性。*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-7A* 和 *QPm.caas-4DL*/*QPm.caas-2BS* 组合的叶锈病 MDS 和 AUDPC 较高, 与鲁麦 21 差异不显著, 但显著高于 21 个聚合株系中其他 7 种 QTL 聚合体($P<0.05$), 其余 4 种 QTL 聚合体抗性与百农 64 无显著差异。

除株系 BFB12 外, 随着含有白粉病抗性 QTL 数量的增多, 聚合株系的条锈病和叶锈病 MDS 和 AUDPC 呈现逐渐降低趋势(图 1)。

表1 21个聚合基因株系及其亲本3种病害的最大严重度(MDS)和病程曲线下面积(AUDPC)

Table 1 Composition of slow mildewing QTL, and averaged MDS and AUDPC for powdery mildew, stripe rust and leaf rust response in 21 F_6 lines from the Bainong 64/Lumai 21 cross and their parents

品系 Line	慢白粉病 QTL Slow mildewing resistance QTL	QTL 数 No. of QTLs	白粉病 Powdery mildew		条锈病 Stripe rust		叶锈病 Leaf rust	
			MDS	AUDPC	MDS	AUDPC	MDS	AUDPC
BN 64	1A/4DL/6BS/7A	4	7.0 cde	45.0 defg	36.8 cdefgh	210.6 efgh	15.8 ef	91.6 ef
LM 21	2BS/2BL/2DL	3	12.0 a	75.3 a	50.0 abcd	290.5 bcde	35.0 a	212.9 a
BFB5	1A/4DL/2BS	3	3.5 f	22.8 hig	33.7 fghi	195.5 fghi	9.4 fgh	52.0 fgh
BFB6	1A/4DL/2DL	3	4.5 ef	33.3 fghi	35.3 fghi	198.6 fghi	9.0 fgh	50.1 fgh
BFB7	1A/4DL/2DL	3	4.0 ef	31.5 fghi	48.0 abcd	288.3 cde	8.7 fgh	48.0 fgh
BFB8	1A/4DL/2DL/2BS/2BL	5	4.3 ef	39 efghi	27.5 ghijk	160.5 ghijk	4.6 h	25.4 gh
BFB9	1A/4DL/2BS/2BL	4	9.5 abc	63.5 abcd	24.7 hijk	143.3 hijk	3.6 h	18.9 h
BFB10	1A/4DL/2DL/2BS/2BL	5	2.8 f	20.8 hi	21.0 hijk	123.7 jk	8.9 gh	48.5 fgh
BFB11	1A/4DL/2DL/2BS	4	2.8 f	17.3 i	18.2 jk	101.6 jk	5.7 gh	31.6 gh
BFB12	4DL/2BS	2	11.3 ab	72.8 ab	36.5 efgh	186.1 fghij	35.7 a	200.7 a
BFB13	1A/4DL/2DL	3	4.0 ef	23.5 hig	31.5 ghij	172.5 ghijk	15.4 ef	87.2 ef
BFB14	1A/4DL/2DL	3	3.8 ef	22.8 hig	16.2 k	91.7 k	10.0 fgh	54.8 fgh
BFB15	1A/4DL/2DL/2BS	4	8.5 bcd	59.3 abcde	54.3 ab	324.2 abcd	26.7 cd	145.8 cd
BFB16	1A/4DL/2BL/7A	4	5.8 def	51.0 abcdef	26.8 ghijk	168.0 ghijk	15.5 ef	83.3 ef
BFB17	1A/4DL/2BL/7A	4	5.0 ef	35.5 fghi	29.7 ghijk	177.7 fghij	14.3 efg	72.9 efg
BFB18	1A/4DL/2DL/2BL/7A	5	5.8 def	43.8 defgh	27.3 ghijk	162.7 ghijk	32.9 bc	182.1 bc
BFB19	1A/4DL/2DL/2BL/7A	5	5.8 def	32.5 fghi	39.5 cdefg	241.6 defg	21.3 de	114.3 de
BFB20	1A/4DL/2BL/7A	4	4.0 ef	32.8 fghi	39.2 cdefgh	227.1 efgh	21.0 de	113.2 de
BFB21	1A/4DL/2DL/2BL/7A	5	5.3 def	47.8 cdef	45.3 cdef	257.9 cdef	27.9 cd	155.8 cd
BFB22	1A/4DL/7A	3	9.8 abc	68.8 abc	53.5 ab	327.1 abc	31.9 bc	175.9 bc
BFB23	1A/4DL/7A	3	11.3 ab	76.5 a	61.7 a	374.5 a	29.2 bcd	158.8 cd
BFB24	1A/4DL/7A	3	10.0 abc	59.0 abcde	57.7 ab	349.7 ab	32.8 bc	179.0 bc
BFB25	1A/4DL/7A	3	7.0 cde	45.0 defg	50.8 abc	316.2 abcd	27.9 cd	157.0 cd

慢白粉病 QTL 由 Lan 等[21-22]鉴定,其中 *QPm.caas-4DL* 缩写为 4DL,余此类推。*QPm.caas-4DL* 和 *QPm.caas-6BS* 兼抗白粉病、条锈病和叶锈病, *QPm.caas-2BS* 和 *QPm.caas-2BL* 兼抗白粉病和条锈病[20,25]。白粉病数据为 2009–2010 和 2010–2011 年度北京和河南安阳两点的平均值[23]。条锈病数据为 2012–2013 年度四川郫县和甘肃天水两点的平均值。叶锈病数据为 2012–2013 年度河北保定和河南周口 2 点的平均值。平均值后不同字母表示品系间差异显著($P < 0.05$)。BN64: 百农 64; LM21: 鲁麦 21。

Slow powdery mildew QTL were mapped by Lan et al. [21-22] QTL 4DL is short for *QPm.caas-4DL* and by analogy for other QTLs. *QPm.caas-4DL* and *QPm.caas-6BS* have significant resistance to powdery mildew, stripe rust and leaf rust; *QPm.caas-2BS* and *QPm.caas-2BL* have significant resistance to powdery mildew and stripe rust[20, 25]. Powdery mildew resistance was the means of evaluation values in Beijing and Anyang of Henan province in 2009–2010 and 2010–2011 cropping seasons [23]. Stripe rust resistance was the means of evaluation values in Pixian of Sichuan province and Tianshui of Gansu province in 2012–2013 cropping season; Leaf rust resistance was the means of evaluation values in Baoding of Hebei province and Zhoukou of Henan province in 2012–2013 cropping season. Values followed by different letters are significantly different at $P < 0.05$. BN64: Bainong64; LM21: Lumai 21.

3 讨论

利用分子标记辅助选择聚合慢病性基因是培育兼抗白粉病、条锈病和叶锈病品种的重要途径。迄今为止，已证实 *Yr18/Lr34/Pm38/Sr57*、*Yr29/Lr46/Pm39/Sr58* 和 *Yr46/Lr67/Pm46/Sr55* 等多个小麦慢病性基因兼抗条锈病、叶锈病、白粉病和秆锈病 [26-29]。同时，还在 1BL、2BS、2BL、3BS、6BS 和 7DS 上发现了多个兼抗条锈病、叶锈病和白粉病的基因簇[30]。这些基因的发现为培育兼抗多种病害的小麦品种提供了可能。CIMMYT 约 60%的小麦品种聚合多个慢病性基因，并已建立通过聚合 *Yr18/Lr34/Pm38/Sr57*、*Yr29/Lr46/ Pm39/Sr58* 和 *Yr46/Lr67/Pm46/Sr55* 等几个慢病性基因，选育兼抗几种病害的持久抗性品种的主要育种策略，运用该策略成功选育出一批兼抗型小麦品种[4]。携带 *Yr18/Lr34/Pm38/Sr57* 基因的材料在 CIMMYT 小麦种质资源中广泛存在，已保持 70 多年的抗性，发展中国家含 *Yr18/Lr34/*

表 2　4 个环境下慢白粉病抗性 QTL 对条锈病和叶锈病的效应及其互作

Table 2　Effects of slow mildewing QTL on stripe rust and leaf rust, and their interactions from four environments

变异来源 Source	*df*	条锈病 Stripe rust		叶锈病 Leaf rust	
		SS	%	*SS*	%
4DL	1	2951.7**	16.9	1514.0**	35.3
6BS	1	306.5	1.8	357	8.3
2BS	1	2469.2**	14.1	—	—
2BL	1	3032.1**	17.3	—	—
2BS × 2BL	1	15.3	0.1	—	—
Env × 4DL	1	82.3	0.5	—	—
Env × 6BS	1	172.9	1.0	22.5	0.5
Env × 2BS	1	330.3	1.9	—	—
Env × 2BL	1	879.1	5.0	—	—
Env	1	174.9	1.0	104.1	0.1
E	102	5652.3		18591	

QPm.caas-4DL 缩写为 4DL, 余此类推; Env: 环境; E: 误差; “%”表示部分平方和占总平方和的百分比, 即可以解释的表型变异。**表示 0.01 的显著水平; “—”表示数据不存在。

QTL 4DL is short for *QPm.caas-4DL*, by analogy for other QTLs; Env: environment; E: error; ** Significant at $P<0.01$; Partial sum of squares as “%” to the total indicates the percentage of partial SS; which can be interpreted as an indication of phenotypic variance explained. “—” indicates that the data does not exist.

表 3　不同慢白粉病抗性 QTL 聚合体对白粉病、条锈病和叶锈病抗性效应

Table 3　Effects of different slow mildewing QTL combinations on powdery mildew, stripe rust, and leaf rust response

QTL 聚合体 QTL combination for powdery mildew	株系数 No. of lines	白粉病 Powdery mildew		条锈病 Stripe rust		叶锈病 Leaf rust	
		MDS	AUDPC	MDS	AUDPC	MDS	AUDPC
1A/4DL/6BS/7A	BN64	7.0 b	45.0 b	36.8 b	210.8 b	15.8 c	91.8 c
2BS/2BL/2DL	LM21	12.0 a	75.3 a	50.0 a	290.8 a	35.0 a	213.3 a
1A/4DL/7A	4	10.5 a	68.3 a	56.0 a	341.8 a	30.5 ab	167.8 b
1A/4DL/2DL/2BL/7A	3	5.6 bc	41.1 bc	37.3 b	220.8 b	27.2 b	151.0 b
1A/4DL/2DL/2BS	2	5.2 bc	38.3 bc	36.5 b	212.8 b	16.5 c	88.8 c
4DL/2BS	1	11.3 a	72.8 a	36.5 b	186.3 bc	35.6 a	201.0 a
1A/4DL/2BL/7A	3	5.5 bc	39.8 bc	31.8 bc	190.8 bc	16.8 c	89.8 c
1A/4DL/2BS	1	3.5 c	27.8 bc	33.7 bc	195.8 bc	9.3 de	52.2 de
1A/4DL/2DL	4	4.1 c	29.9 bc	32.8 bc	187.8 bc	10.8 cd	60.0 cd
1A/4DL/2BS/2BL	1	9.5 a	63.5 a	24.7 c	143.7 c	3.5 e	18.8 e
1A/4DL/2DL/2BS/2BL	2	3.5 c	22.8 c	24.5 c	142.2 c	6.8 de	37.0 de

QPm.caas-4DL 缩写为 4DL, 余此类推; 白粉病数据为 2009–2010 和 2010–2011 年度北京和河南安阳两点的平均值[23]。条锈病数据为 2012–2013 年度四川郫县和甘肃天水 2 点的平均值。叶锈病的数据为 2012–2013 年度河北保定和河南周口两点的平均值。平均值后不同字母表示 QTL 聚合体之间差异显著($P<0.05$)。BN64: 百农 64; LM21: 鲁麦 21。

QTL 4DL is short for *QPm.caas-4DL* and by analogy for other QTLs. Powdery mildew resistance was the means of evaluation values in Beijing and Anyang of Henan province in 2009–2010 and 2010–2011 cropping seasons [23]. Stripe rust resistance was the means of evaluation values in Pixian of Sichuan Province and Tianshui of Gansu Province in 2012–2013 cropping season; Leaf rust resistance was the means of evaluation values in Baoding of Hebei province and Zhoukou of Henan province in 2012–2013 cropping season. Values followed by different letters are significantly different at $P < 0.05$. BN64: Bainong 64; LM21: Lumai 21.

Pm38/Sr57 的小麦品种种植面积约有 2600 万公顷[31], 在病害流行年份发挥着重要作用。美国、澳大利亚和欧洲的研究重点近年也从垂直抗性逐步转向慢病性[32-34]。

百农 64 含有的抗白粉病 *QPm.caas-4DL* 与 *Yr46/Lr67/Pm46/Sr55* 很可能为同一基因, 虽然 *Yr46/Lr67/Pm46/Sr55* 抗性效应不及 *Yr18/Lr34/Pm38/Sr57*, 但百农 64 的农艺性状良好, 该位点将是小麦持久抗

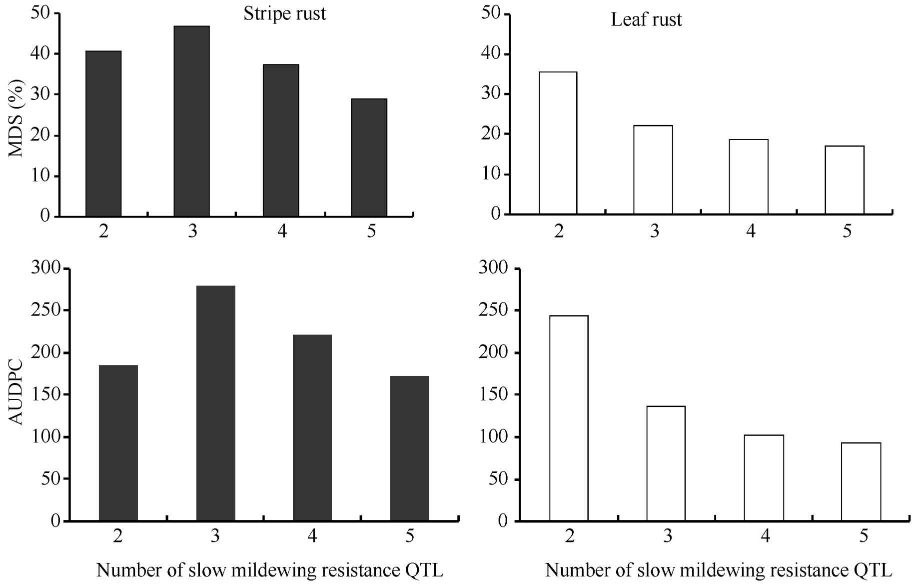

图 1　不同数量慢白粉病抗性 QTL 对条锈病和叶锈病的抗性效应

Fig. 1　Effects of slow mildewing resistance QTL number on reducing stripe rust and leaf rust

病育种的另一重要基因资源。Ren 等[25]在 *QPm.caas-6BS* 同一位置分别发现条锈病和叶锈病抗性QTL，该位点是一个新发现的兼抗多种病害的位点。任妍[20]在鲁麦 21 中定位了 2 个条锈病抗性 QTL *QYr.caas-2BS* 和 *QYr.caas-2BL*，分别与抗白粉病 *QPm.caas-2BS* 和 *QPm.caas-2BL* 位置一致，这两个位点也是小麦持久兼抗育种的重要基因。利用慢病性基因容易做到兼抗与持久抗性的结合，兼抗几种病害的慢病基因都具有持久抗性(Ravi Singh，个人交流)。已经定名的几个慢病性基因(如 *Yr18/Lr34/Pm38/Sr57*、*Yr29/Lr46/Pm39/Sr58* 和 *Yr46/Lr67/Pm46/Sr55* 等)都具有这种特点。我国小麦白粉病、条锈病和叶锈病发生严重，选育兼抗多种病害小麦品种对于我国小麦生产具有重要意义。来自百农 64 的 *QPm.caas-4DL*、*QPm.caas-6BS* 和来自鲁麦 21 的 *QPm.caas-2BL* 和 *QPm.caas-2BS* 等对条锈病、叶锈病和白粉病皆表现慢病性，利用这些基因选育兼抗多种病害的小麦品种可取得事半功倍的效果。虽然过去国内也有育成兼抗且具有持久抗性的小麦品种，但有目的地进行这种育种的尚不多。

在 21 个聚合株系中，含有抗病 QTL 数量较多的株系的 MDS 和 AUDPC 值均较低，表明 QTL 加性效应起了重要作用。Singh 等[7]发现聚合 4~5 个微效基因的小麦材料对条锈和叶锈病呈高抗至免疫。但是，QTL 聚合体的遗传效应并不总是与所含抗病 QTL 的数量成正比。如株系 BFB12 和 BFB14 分别含有 2 个和 3 个抗性 QTL，但条锈病 MDS 和 AUDPC 值均较低。其原因可能是不同的 QTL 聚合体效应不同，部分 QTL 间互作会产生加性效应，或者某些株系含有未知的抗性 QTL，导致条锈病和叶锈病 MDS 和 AUDPC 值较低，抗性增强。

任妍[20]在鲁麦 21 中还发现另外 2 个条锈病抗性 QTL (*QYr.caas-4DL.2* 和 *QPm.caas-2DS.2*)，我们推测本研究的部分株系可能含有这 2 个 QTL，导致 BFB12 和 BFB14 等含有较少兼抗型 QTL 的株系抗性较强。相同 QTL 聚合体的株系抗性并不完全一致，如 BFB11 和 BFB15 均含有 *QPm.caas-1A*/*QPm.caas-4DL*/ *QPm.caas-2DL*/*QPm.caas-2BS* 基因组合，但 BFB11 抗性远大于 BFB15，估计 BFB11 含有其他条锈病抗性 QTL 或存在 QTL 间互作。但综合 21 个株系数据来看，株系含有 QTL 越多，对多种病害的抗性越强。

结合 Bai 等[23]对 21 个聚合株系的白粉病鉴定结果进行分析，株系 BFB5、BFB7、BFB8、BFB10、BFB11 和 BFB14 对白粉病、条锈病和叶锈病均具有较高的抗性，可作为育种亲本材料用于小麦抗锈病和白粉病育种。*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2DL*/*QPm.caas-2BS*/*QPm.caas-2BL*、*QPm.caas-1A*/*QPm.caas-4DL*/*QPm.caas-2DL* 和 *QPm.caas-1A*/*QPm.caas-4DL*/ *QPm.caas-2BS* 组合对白粉病、条锈病和叶锈病均具有较好的抗性，是选育兼抗多种病害小麦慢病性品种的良好材料。*QPm.caas-1A*/*QPm.caas-4DL*/ *QPm.caas-2BS*/*QPm.caas-2BL* 对条锈病和叶锈病抗性较好，可用于条锈病和叶锈病多发区的抗病

育种。

4　结论

6 个聚合百农 64 和鲁麦 21 慢白粉病抗性 QTL 的 F_6 株系对白粉病、条锈病和叶锈病均具有较好的慢病性，且农艺性状优良，是选育抗病高产品种的优良材料。证实了利用分子标记进行慢病性 QTL 聚合的可行性及其有效性，进一步说明聚合 4~5 个慢病性 QTL 足以在田间表现高水平抗性，为小麦抗病育种提供了材料和育种思路。

References

[1] Wellings C R, Mcintosh R A, Hussain M. A new source of resistance to *Puccinia striiformis* f. sp. *tritici* in spring wheats (*Triticum aestivum*). *Plant Breed*, 1988, 100: 288–296

[2] Komer J A. Genetics of resistance to wheat leaf rust. *Annu Rev Phytopathol*, 1996, 34: 435–455

[3] Conner R L, Kuzyk A D, Su H. Impact of powdery mildew on the yield of soft white spring wheat cultivars. *Can J Plant Sci*, 2003, 83: 725–728

[4] Singh R P, Huerta-Espino J, William H M. Genetics and breeding for durable resistance to leaf and stripe rusts in wheat. *Turk J Agric For*, 2005, 29: 121–127

[5] Roberts J, Caldwell R M. General resistance (slow mildewing) to *Erysiphe graminis* f. sp. *tritici* in Knox wheat. *Mol Gen Genet*, 1970, 60: 1310

[6] Gustafson G D, Shaner G. Influence of plant age on the expression of slow-mildewing resistance in wheat (*Triticum aestivum*). *Phytopathology*, 1982, 72: 746–749

[7] Singh R P, Huerta-Espino J, Bhavani S, Herrera-Foessel S A, Singh D, Singh P K, Velu G, Mason R E, Jin Y, Njau P, Crossa J. Race non-specific resistance to rust diseases in CIMMYT spring wheats. *Euphytica*, 2011, 179: 175–186

[8] Lu Y M, Lan C X, Liang S S, Zhou X C, Liu D, Zhou G, Lu Q L, Jing J X, Wang M N, Xia X C, He Z H. QTL mapping for adult-plant resistance to stripe rust in Italian common wheat cultivars Libellula and Strampelli. *Theor Appl Genet*, 2009, 119: 1349–1359

[9] Lan C X, Liang S S, Zhou X C, Zhou G, Lu Q L, Xia X C, He Z H. Identification of genomic regions controlling adult-plant stripe rust resistance in Chinese landrace Pingyuan 50 through bulked segregant analysis. *Phytopathology*, 2010, 100: 313–318.

[10] Krattinger S G, Lagudah E S, Spielmeyer W, Singh R P, Huerta-Espino J, Mcfadden H, Bossolini E, Selter L L, Keller B. A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. *Science*, 2009, 323: 1360–1363

[11] Bhavani S, Singh R P, Argillier O, Huerta-Espino J, Singh S, Njau P, Brun S, Lacam S, Desmouceaux N. Mapping Durable Adult Plant Stripe Rust Resistance to the Race Ug99 Group in Six CIMMYT Wheats. BGRI 2011 Technical Workshop, St. Paul, Minnesota, 2011. pp 44–53

[12] Singh R P, Huerta-Espino J, Rajaram S. Achieving near-immunity to leaf and stripe rusts in wheat by combining slow rusting resistance genes. *Acta Phytopathol Entomol Hung*, 2000, 35: 133–139

[13] Castro A J, Chen X M, Hayes P M, Johnston M. Pyramiding quantitative trait locus (QTL) alleles determining resistance to barley stripe rust: effects on resistance at the seedling stage. *Crop Sci*, 2003, 43: 651–659

[14] Marasas C N, Smale M, Singh R P. The impact of agricultural maintenance research: the case of leaf rust resistance breeding in CIMMYT-related spring bread wheat. In: CD-ROM Proceeding Internal Congress on Impacts of Agricultural Research and Development. San Jose, Costa Rica, 2002

[15] Singh R P, William H M, Huerta-Espino J, Rosewarne G. Wheat rust in Asia: meeting the challenges with old and new technologies. In: New Directions for a Diverse Planet. Proceedings of the 4th International Crop Science Congress. Brisbane, Australia, 2004, p 26

[16] Dekkers J C M, Hospital F. The use of molecular genetics in the improvement of agricultural populations. *Nat Rev Genet*, 2003, 3: 22–32

[17] Miedaner T, Wilde F, Steiner B, Buerstmayr H, Korzun V, Ebmeyer E. Stacking quantitative trait loci (QTL) for *Fusarium* head blight resistance from non-adapted sources in an European elite spring wheat background and assessing their effects on deoxynivalenol (DON) content and disease severity. *Theor Appl Genet*, 2006, 112: 562–569

[18] Lu Q X, Szabo-Hever A, Åsmund B, Lillemo M, Semagn K, Mesterhazy A, JiF, Shi J R, Skinnes H. Two major resistance quantitative trait loci are required to counteract the increased susceptibility to *Fusarium* head blight of the *Rht-D1b* dwarfing gene in wheat. *Crop Sci*, 2011, 51: 2430–2438

[19] Wang Z L, Li L H, He Z H, Duan X Y, Zhou Y L, Chen X M, Lillemo M, Singh R P, Wang H, Xia X C. Seeding and adult-plant resistance to powdery mildew in Chinese bread wheat cultivars and lines. *Plant Dis*, 2005, 89: 457–463

[20] 任妍. 普通小麦抗条锈病基因分子定位. 中国农业科学院博士学位论文, 北京, 2012. pp 56–63
Ren Y. Molecular Mapping of Stripe Rust Resistance Genes in Common Wheat. PhD Dissertation of Chinese Academy of Agricultural Sciences, Beijing, China, 2012. pp 56-63 (in Chinese with English abstract)

[21] Lan C X, Liang S S, Wang Z L, Yan J, Zhang Y, Xia X C, He Z H. Quantitative trait loci mapping for adult-plant resistance to powdery mildew in Chinese wheat cultivar Bainong 64. *Phytopathology*, 2009, 99: 1121–1126

[22] Lan C X, Ni X W, Yan J, Zhang Y, Xia X C, Chen X M, He Z H. Quantitative trait loci mapping of adult-plant resistance to powdery mildew in Chinese wheat cultivar Lumai 21. *Mol Breed*, 2010, 25: 615–622

[23] Bai B, He Z H, Asad M A, Lan C X, Zhang Y, Xia X C, Yan J, Chen X M, Wang C S. Pyramiding adult-plant powdery mildew resistance QTLs in bread wheat. *Crop Pasture Sci*, 2011, 63: 606–611

[24] Lin F, Chen X M. Quantitative trait loci for non-race-specific, high-temperature adult-plant resistance to stripe rust in wheat cultivar Express. *Theor Appl Genet*, 2009, 118: 631–642

[25] Ren Y, Li Z F, He Z H, Wu L, Bai B, Lan C X, Wang C F, Zhou G, Zhu H Z, Xia X C. QTL mapping of adult-plant resistance to

stripe rust and leaf rust in Chinese wheat cultivar Bainong 64. *Theor Appl Genet*, 2012, 125: 1253–1262

[26] Lillemo M, Asalf B, Singh R P, Huerta-Espino J, Chen X M, He Z H, Bjørnstad Å. The adult plant rust resistance loci *Lr34/Yr18* and *Lr46/Yr29* are important determinants of partial resistance to powdery mildew in bread wheat line Saar. *Theor Appl Genet*, 2008, 116: 1155–1166

[27] Singh R P. Genetic association of leaf rust resistance gene *Lr34* with adult plant resistance to stripe rust in bread wheat. *Phytopathology*, 1992, 82: 835–838

[28] Dyck P L, Kerber E R, Aung T. An interchromosomal reciprocal translocation in wheat involving leaf rust resistance gene *Lr34*. *Genome*, 1994, 37: 556–559

[29] Herrera-Foessel S A, Lagudah E S, Huerta-Espino J, Hayden M, Bariana H S, Singh R P. New slow-rusting leaf rust and stripe rust resistance gene *Lr67* and *Yr46* in wheat are pleiotropic or closely linked. *Theor Appl Genet*, 2011, 122: 239–249

[30] 何中虎, 兰彩霞, 陈新民, 邹裕春, 庄巧生, 夏先春. 小麦条锈病和白粉病成株抗性研究进展和展望. 中国农业科学, 2011, 44: 2193–2215
He Z H, Lan C X, Chen X M, Zou Y C, Zhuang Q S, Xia X C. Progress and perspective in research of adult-plant resistance to stripe rust and powdery mildew in wheat. *Sci Agric Sin*, 2011, 44: 2193–2215 (in Chinese with English abstract)

[31] Marasas C N, Smale M, Singh R P. The economic impact of productivity maintenance research: breeding for leaf rust resistance in modern wheat. *Agric Eco*, 2003, 29: 253–263

[32] Chen X M, Line R F. Gene action in wheat cultivars for durable high-temperature adult-plant resistance and interactions with race-specific, seedling resistance to stripe rust caused by *Puccinia striiformis*. *Phytopathology*, 1995, 85: 567–572

[33] Bariana H S, Kailasapillai S, Brown G N, Sharp P J. Marker assisted identification of *Sr2* in the National Cereal Rust Control Program in Australia, In: Slinkard A E ed. Proc 9th Intl Wheat Genet Symp. Vol. 5. University of Saskatchewan, Saskatoon, SK, Canada: Univ. Extension Press, 1998. pp 83−91

[34] Keller M, Keller B, Schachermayr G, Winzeler M, Schmid J E, Stamp P, Messmer M M. Quantitative trait loci for resistance against powdery mildew in a segregating wheat × spelt population. *Theor Appl Genet*, 1999, 98: 903–912