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葡萄遗传图谱构建与抗病QTL定位研究进展

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摘 要:葡萄在生长发育过程中易遭受多种病原菌的侵染,影响果实品质和产量,制约葡萄产业的发展。生产中多采用杀菌剂对病原菌进行防治,增加了投资成本,且会对环境造成污染,因此培育高品质抗病品种对葡萄生产具有重要意义。葡萄抗病性为多基因控制的数量性状,QTL定位是研究数量性状的一种有效方法,遗传图谱的构建是检测QTLs和克隆基因的基础。多年来,研究人员通过构建遗传图谱鉴定了一系列霜霉病、白粉病、皮尔斯病等抗性遗传位点,同时,根据抗性位点的基因组区域,开发了多个连锁标记,并应用到葡萄抗病性遗传研究中,加速了葡萄的育种进程。对葡萄遗传连锁图谱的构建和抗病相关QTL定位研究进展进行了综述,分析了目前研究中存在的问题并提出建议,为今后葡萄抗病基因定位和分子标记辅助选择育种提供借鉴。

关键词:葡萄;遗传图谱;抗病;QTL定位

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Research progress in genetic map construction and QTL mapping for disease resistance in grapevine

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Abstract: Grape is one of the most important horticultural crops in the world, which has been cultivated as a source of fresh fruit, raisins, wine and distilled beverages. In recent years, our country's grape production has increased rapidly, ranking first in the world. However, the grape is susceptible to infection by a variety of pathogens during the growth and development process, which affects berry quality and yield and restricts the development of the grape industry. Control of pathogenss requires regular application of fungicides. Nevertheless, the intensive use of chemicals becomes more and more restrictive because of their cost, risk on human health and negative environmental impact. Therefore, plant breeding for disease resistance is the most attractive way to control grapevine pathogens effectively and environment- friendly. The grape has the characteristics of long childhood and high heterozygosity and breeding for disease resistance is a very time-consuming process, because it needs the evaluation of resistance levels of the progeny. Molecular marker assistant selection (MAS) technology can improve the efficiency of directional breeding and accelerate the breeding process. Grape disease resistance is a quantitative trait controlled by multiple genes. QTL mapping is an effective method to study quantitative traits. The construction of a genetic map is the basis for detecting QTLs and cloning genes. Since Lodhi built the first genetic map of grapevines based on RAPD marker and AFLP marker, more than 160 grape genetic maps have been published in the world, of which 40 are related to grape disease resistance. Mapping populations and molecular markers are two key factors in constructing the genetic maps. The QTL mapping study is usually carried out in the crossed F_1 generation population, and a few

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are self-crossed and backcrossed populations. The early grape genetic map was mainly constructed using AFLP and RAPD molecular markers, but different maps could not be compared, and the limitations were large. Subsequently, with the development of sequencing technology, because of its co-dominance and high polymorphism, simple sequence repeat (SSR) markers have high versatility among different grape varieties, and has become the most frequently used marker for constructing the disease resistance genetic maps. However, the limited number of SSR markers and the limited density and precision of genetic maps cannot effectively map candidate genes associated with traits. Single nucleotide polymorphism (SNP) markers are evenly distributed in the genome and have a large number, which can avoid the problem of low map marker density and significantly improve the degree of fine mapping. In recent years, it has been widely used in the construction of genetic maps. Overall, the size of the mapping population in the grape genetic map study was more than 100, and the number and density of disease resistance genetic map markers continued to increase so that the average distance between markers decreased from 12.7 cM to 0.28 cM. Over the years, researchers have identified a series of disease resistance genetic loci. As a global fungal disease, grape downy mildew has the most researched resistance loci. Currently, 28 major or minor resistance loci have been located on chromosomes 4, 5, 6, 7, 8, 9, 10, 12, 14, 17 and 18, which explained phenotypic variation ranging from 3.5% to 86.3%. Grape powdery mildew is a fungal disease caused by the pathogenic fungus *Erysiphe necator* [synonym *Uncinula necator* (Schw.) Burr.], which can cause leaves to turn chlorotic and cover with a white powdery layer, resulting in leaf curling, wilting and other symptoms. Grape powdery mildew resistance loci are much more as downy mildew researches are conducted, named Run (Resistance to *Uncinula necator*) or Ren (Resistance to *Erysiphe necator*). The current powdery mildew resistance loci are 2 (Ren10), 9 (Ren6), 12 (Run1), 14 (Ren2, Ren5), 15 (Ren3, Ren9), 13 (Ren1), 18 (Run2.1, Run2. 2, Ren4, Ren8) and 19 (Ren7) chromosomes, which are identified, explained phenotypic variation ranging from 14% to 76%. Other grape diseases, such as Pierce's disease, crown gall disease, black rot, ripe rot, white rot, etc., also harm grapes, but there are relatively few studies on QTL mapping. These localization results have laid the foundation for the use of molecular markers in breeding. Based on the genomic region of the resistance loci, multiple linkage markers have been developed and applied to the genetic research on grape disease resistance and the grape breeding process has been accelerated. In recent years, the construction of grape disease resistance genetic map has developed rapidly, and some achievements have been obtained, but there are still problems. In this paper, we summarized the research progress in the construction of the genetic linkage map of grapes and the location of QTLs related to disease resistance. Meanwhile, the existing problems in the current research were also analyzed and discussed. This would provide an important reference for future grape disease resistance mapping and molecular marker-assisted selection breeding.

Key words: Grape; Genetic mapping; Disease resistance; Quantitative trait locus (QTL)

葡萄是多年生落叶藤本植物，果实风味浓郁，营养价值高，既可鲜食，也可加工成各种产品，在农业经济中发挥着重要作用。据世界粮农组织（FAO，2020）统计，中国葡萄产量达1 476.9万t，居世界第一位。葡萄生长过程中各种生物或非生物胁迫对产量有着较大影响，由病原菌引起的生物胁迫是非常严重的危害因子[1]。目前葡萄生产上对病原菌治理主要是药剂防治，不仅增加栽培成本，更危害环境及食品安全[2]，培育抗病品种有利于葡萄产业健康发展。葡萄具有童期长、杂合度高等特点，使用常规育种耗时长、效率低，通过分子标记辅助选择育种（molecular marker assistant selection，MAS）技术能提高定向育种效率，加速育种进程[3]。

构建遗传连锁图谱（genetic linkage map），进行

数量性状位点（quantitative trait locus，QTL）定位，建立标记与表型之间的连锁关系，是实施分子标记辅助育种的有效途径[4]。自Lodhi等[5]基于随机扩增多态性DNA标记（random amplified polymorphic DNA，RAPD）和扩增片段长度多态性标记（amplified fragment length polymorphism，AFLP）构建了第一张葡萄遗传图谱以来，世界上已经发布了160多张葡萄遗传图谱[6]，其中约40张与葡萄抗病性有关。以遗传连锁图谱为基础，研究人员已对多个葡萄抗病相关位点进行定位，并开发了连锁标记，部分已经应用于育种中[7]。笔者在本文中对葡萄遗传图谱构建与抗病QTL定位的研究进展进行综述，为葡萄抗病性定位相关研究和分子标记辅助选择育种提供借鉴和参考。

1　葡萄遗传图谱的构建

构建高密度遗传图谱是进行基因定位、分子标记辅助育种，以及图位克隆的基础[8]。构建遗传图谱主要包括选择合适的作图群体、采用多态性分子标记以及根据重组率利用相关作图软件计算分子标记间的连锁排序和遗传距离。

作图群体的选择是构建遗传图谱的前提。目前F_1群体、F_2群体、BC群体、DH群体、RIL群体（重组自交系）等作图群体在QTL定位研究中均有使用[3,9]。但葡萄童期长、纯合与杂合位点共存、遗传背景复杂等问题难以获得高世代群体。针对这一问题，Weeden等[10]提出了著名的“双假测交”理论，即将F_1杂交群体视为与隐性亲本测交得到的回交一代（BC_1）群体。当F_1群体出现分离重组，其分离重组发生在亲本所特有遗传标记位点，则将其中一个亲本的杂合位点看作是另一个亲本的隐性纯合，后代群体1∶1分离，则相当于“测交”；若分离重组位于两亲本共有的标记位点，则将两亲本都视为杂合位点，如若是共显性标记，后代群体分离比为1∶2∶1，若是显性标记后代，分离比则为3∶1。基于此理论，葡萄常用于构建遗传图谱的群体类型主要为杂交F_1代，少数为回交群体、自交群体。葡萄F_1代杂交群体虽易于构建，可以缩短定位群体建立周期，但该群体属于暂时分离群体仅能使用一次，遗传背景复杂容易造成定位偏差[9]。

分子标记由于变异丰富、稳定、不受环境影响等因素成为葡萄遗传图谱研究的有效手段。早期葡萄遗传图谱主要采用RAPD和AFLP分子标记进行构建。1995年Lodhi等[5]利用Cayuga White × Aurore的F_1群体，结合RAPD和AFLP等标记构建2张遗传图谱，其中Cayuga White构成的遗传图谱包含214个标记，全长为1196 cM；Aurore构成的遗传图谱包含225个标记，全长为1477 cM。这两种标记可以快速构建图谱，但构建的不同葡萄品种的遗传图谱之间无法比较[11]，局限性较大。随着测序技术的发展，简单序列重复标记（simple sequence repeat，SSR）因共显性、高度多态性，在不同葡萄品种间具有较高的通用性，成为构建遗传图谱使用频率最高的标记。葡萄第一套SSR标记（共371个）由葡萄微卫星联盟（Vitis Microsatellite Consortium，VMC）开发[11]。Riaz等[12]利用Riesling × Cabernet Sauvignon杂交群体结合152个SSR标记（主要来自VMC）构建了第一张葡萄SSR遗传图谱，该图谱总长为1728 cM，标记间平均距离为11.0 cM。Di Gaspero等[13]开发了另外两组基于微卫星的标记（169个VVI和108个UDV）。Adam-Blondon等[14]以Syrah × Grenache的F_1群体为材料，利用220个SSR标记（包含123个VVI标记）构建了总长度为1 406.1 cM、标记平均距离为6.4 cM的遗传图谱。为了提高SSR标记构建图谱的饱和度、通用性和实用性，Doligez等[15]将5个遗传群体整合得到一张含515个标记（502个SSR标记）的遗传图谱，该图谱总长度为1647 cM，标记间平均距离为3 cM。此图谱是基于SSR标记最为完整的图谱之一。但SSR标记数量有限[16]，遗传图谱密度和精度受限，无法对性状相关的候选基因进行有效定位[11]。伴随着测序技术的发展，单核苷酸多态性（single nucleotide polymorphisms，SNP）标记越来越多地被应用在遗传图谱构建上。相较之前的标记，SNP在基因组均匀分布，多态性好，可以避免图谱标记密度偏小的问题，显著提高精细定位程度[6,17]。全基因组测序（whole genome sequencing）、简化基因组测序（reduced-representation genome sequencing，RRGS）和SNP-array是开发SNP标记的主要高通量测序技术。Sapkota等[1]用Norton × Cabernet Sauvignon的159个F_1单株为作图群体，结合1665个SNP标记和407个SSR标记获得抗霜霉病遗传图谱。Sun等[18]利用Red Globe × Muscat Hamburg的95个F_1群体，结合27 454个SNP标记，构成覆盖长度为1 442.64 cM

的遗传图谱。Su等[19]利用Zhuosexiang × Victoria的F_1代群体，采用6249个SNP构建的抗白腐病整合图谱大小为3 118.13 cM，平均标记密度是0.5 cM。最近，一种基于扩增子测序（AmpSeq）的新型高效分子标记应用于遗传图谱的构建。Karn等[20]利用Horizon × Illinois 547-1的F_1群体，构建一张包含1171个Ampseq标记、覆盖总长度为1 082.16 cM的图谱。Reshef等[21]利用 *V. rupestris* B38 × Horizon的杂交群体，构建一张包含1944个Ampseq标记、总长度范围为1 050.7 cM的遗传图谱。葡萄主要图谱的基本情况见表1。从表1可以看出，国内外对葡萄遗传图谱研究中作图群体数量大多在100株以上；标记类型从最初的AFLP标记到大规模测序开发SNP标记，不断向前发展；遗传图谱标记数目和密度不断增加，使得标记之间的平均距离从12.7 cM降至0.28 cM。

表1 葡萄主要遗传连锁图谱

Table 1 Main genetic linkage maps of grape

亲本 Parents	作图群体 Mapping population	群体大小 Population size	图谱长度 Mapping distance/cM	标记类型 Marker types	标记数 Marker numbers	平均距离 Average distance/cM	参考文献 Reference
Syrah×28-8-78	BC2	139	–	RAPD、ISSR、SSR	372	–	[22]
MTP2223-27 ×MTP2121-30	F_1	139	233.00	AFLP、SSR	1204	5.60	[23]
MTP2687-85×Muscat of Hamburg	F_1	174	119.00	SSR	1267	12.70	[24]
D8909-15×F8909-17	F_1	87	1154.00	SSR、RFLP	210	5.50	[25]
Regent×Lemberger	F_1	144	1631.00	AFLP、SSR、RGA、SCAR	398	4.67	[26]
CabernetSauvign×Gloire de Montpellier	F_1	138	1249.00	SSR、SSCP	212	6.70	[3]
Italia × Big Perlon	F_1	163	1426.00	SSR、AFLP、EST、SCAR	341	4.20	[27]
Moscato Bianco×W63	F_1	174	1 037.20	SSR、EST、RGA	164	7.30	[28]
V3125 × Börner	F_1	202	1 364.90	SSR	374	3.90	[29]
Ramsey × Riparia Gloire	F_1	188	1 304.70	SSR	205	6.80	[30]
VRH 3082 1-42×SK77 5/3	F_1	94	651.00	SSR、EST、RGA、SNP	133	6.00	[28]
Merzling×Teroldego	F_1	89	1 309.20	SSR、SNP	247	5.40	[31]
Ruprecht×Ruprecht	F_1	232	975.00	SSR、RGA	133	7.30	[32]
Gf.Ga-52-42×Solar	F_1	265	1 097.28	SSR	208	6.27	[33]
GF.V3125×BOERNER	F_1	202	–	SSR	–	–	[34]
F2-35×DVIT202	F_1	277	1005.42	SSR	208	4.83	[35]
GF.GA-47-42×Villard blanc	F_1	151	1 324.10	SSR、SNP	543	2.71	[36]
Muscat of Alexandria×Muscat à Petits Grains Blancs	F_1	95	1 257.40	SSR	338	4.60	[37]
Norton×Cabernet Sauvignon	F_1	159	2 203.50	SSR、SNP	2072	1.10	[1]
Black Beauty×Nesbitt	F_1	172	1 633.60	SNP	1224	1.30	[38]
Cabernet sauvignon × Zuoyouhong	F_1	181	1 780.48	SNP	25 917	0.41	[39]
Cabernet Sauvignon×Shuang Hong	F_1	91	1 665.31	SNP	934	1.81	[40]
Red Globe×Shuangyou	F_1	149	1 929.13	SNP、INDEL	7199	0.28	[41]
Red Globe× Muscat Hamburg	F_1	95	1 442.64	SNP	27 454	0.93	[18]
Cabernet Sauvignon×Shuang Hong	F_1	91	1 898.09	SNP	5603	0.45	[42]
Zhuosexiang×Victoria	F_1	177	3 118.13	SNP	6294	0.43	[19]
PI588160×PI58827	F_1	294	1 634.10	SNP	2583	0.63	[43]
Horizon × Illinois 547-1	F_1	142	1 082.16	rhAmpSeq	1171	1.01	[20]
B38 × Horizon	F_1	118	1 050.70	rhAmpSeq	1944	1.10	[21]

注：“–”表示该文献无此内容。下同。

Note: “–” means no relevant content is shown in this reference. The same below.

构建遗传图谱需将分子标记分配到不同的连锁群，每个连锁群内根据重组率对标记进行排序并估计遗传距离。目前常用的构图软件有JoinMap、Mapmaker和TMAP等[6,44]。但同一作图软件不会包含所有分离类型，不同软件构建的遗传图谱也存在差异，应根据实际情况进行选择。

2　抗病性状QTL定位

2.1　葡萄霜霉病抗性QTL定位

葡萄霜霉病作为全球性真菌性病害，抗性位点研究最多。Merdinoglu等[22]利用Syrah×28-8-78的F_1分离群体进行抗霜霉病QTL分析，首次在28-8-78的12号染色体上鉴定到一个主效QTLRpv1（Resistance to *Plasmopara viticola* 1），该位点能够解释73%的表型变异，与其紧密连锁的标记为VVIb32。来源于圆叶葡萄的Rpv1抗性基因已被克隆并进行了功能验证。*Rpv*1是核苷酸结合/富含亮氨酸重复（nucleotide binding/leucine-rich repeat，NB-LRR）受体，参与病原菌的识别和植物防御的信号转导[45-46]。Welter等[26]利用Regent ×Lemberge的F_1代群体通过4年霜霉病抗性鉴定，最终在18号染色体中得到1个主效QTLRpv3，该位点解释了37.3%表型差异，富含TIR-NBS-LRR基因，并在不同群体的研究中得到进一步验证[22,47]。含有*Rpv*3位点的葡萄植株叶片在受到霜霉病侵染时，霜霉病菌丝体生长受限，新生孢子囊和孢子囊数量减少[48-49]。Marguerit等[3]通过Cabernet Sauvignon × Gloire De Montpellie的F_1子代霜霉病抗性鉴定，发现在9和12号染色体存在2个抗性位点Rpv5和Rpv6，其中Rpv5紧密连锁的标记VVIO52；Rpv6是第二个定位在12号染色体上抗性位点。Bellin等[47]使用Chardonnay × Bianca群体通过多种霜霉病表型鉴定方法，发现Bianca的7号染色体上存在抗性位点Rpv7，该位点解释的表型变异率为12.7%。Blasi等[32]使用雌雄同株山葡萄品种（*V. amurensis* ‘Ruprecht’）自交后代，通过5种抗性评价体系，在14号染色体上发现抗性位点Rpv8，该位点解释的表型变异率高达86.3%。Schwander等[33]将Rpv10定位在9号连锁群，并将其范围精确定位到2.1 cM，大小为314 kb。研究还发现该区域包含8个核苷酸结合/富含亮氨酸重复（nucleotide binding/leucine-rich repeat，NBS-LRR）类型的RGA。随后越来越多的抗霜霉病位点被挖掘，目前，在4、5、6、7、8、9、10、12、14、17和18号染色体上共定位到28个抗性主效或微效QTL（表2），解释的表型变异率从3.5%到

表2　霜霉病抗性位点

Table 2　Downy mildew resistance site

位点 Locus	亲本 Parents	染色体 Chromosome	位置 Position/Mb	紧密连锁标记 Associated marker	表型变异率 Phenotypic variance/%	参考文献 Reference
Rpv1	Syrah×28-8-78	12	10.3	VVIb32	73.00	[22]
Rpv2	Cabernet Sauvignon ×8624	18	–	–	21.00	[32]
Rpv3	Chardonnay×Bianca	18	–	UDV112	37.30	[26]
Rpv4	Regent×Lemberger	4	4.7	VMC7H3	22.60	[26]
Rpv5	Cabernet Sauvignon × Gloire De Montpellie	9	4.0	VVIO52	34.40	[3]
Rpv6	Cabernet Sauvignon × Gloire De Montpellie	12	20.4	VMC8G9	31.50	[3]
Rpv7	Chardonnay × Bianca	7	11.4	UDV097	12.70	[47]
Rpv8	Ruprecht×Ruprecht	14	6.6	Chr14V015	86.30	[32]
Rpv9	Moscato Bianco×W63	7	16.6	IN0006	21.10	[26]
Rpv10	GF.GA-52-42×Solaris	9	3.7	GF09-46	50.00	[33]
Rpv11	Regent ×Lemberger	5	4.5	VCHR05C	3.50	[33]
Rpv12	99-1-48 × Pinot Noir	14	8.0	UDV014	78.70	[50]
Rpv13	Moscato Bianco×W63	12	10.0	VMC1G3.2	21.20	[28]
Rpv14	GF.V3125 ×Boerner	5	20.2	GF05-13	17.40	[51]
Rpv17	B38×Horizon	8	11.7	–	12.94	[52]
Rpv18	B38×Horizon	11	15.4	–	8.77	[52]
Rpv19	B38×Horizon	14	29.5	–	15.14	[52]
Rpv20	Horizon×B9	6	0.9	–	8.37	[52]
Rpv21	Horizon×B9	7	2.1	–	11.77	[52]
Rpv25	RedGlobe×Shuangyou	15	3.0	Marker561 375	18.60	[41]
Rpv26	RedGlobe×Shuangyou	15	15.0	Marker525 926	63.60	[41]
Rpv27	Norton×Cabernet Sauvignon	18	26.0	UDV737	33.80	[1]
Rpv28	PI588160×PI58827	10	–	S10_1 285 522	66.50	[43]

86.3%。这些QTL抗性位点来源于不同的葡萄品种。Rpv1和Rpv2来源于圆叶葡萄(*Muscadinia rotundifolia*);Rpv3、Rpv19和Rpv28来源于沙地葡萄(*V. rupestris*);Rpv4、Rpv7、Rpv11、Rpv17、Rpv18、Rpv20和Rpv21来源于北美种群但未确定品种;Rpv5、Rpv6、Rpv9和Rpv13来源于河岸葡萄(*V. riparia*);Rpv8、Rpv10、Rpv12、Rpv22、Rpv23、Rpv24、Rpv25和Rpv26来源于山葡萄(*V. amurensis*);Rpv14来源于甜冬葡萄(*V. cinerea*); Rpv27来源于夏葡萄(*V. aestivalis*)。这表明利用优异的种质资源去挖掘更丰富的优异变异,是寻找葡萄抗病基因的重要途径。

2.2 葡萄白粉病抗性QTL定位

葡萄白粉病是由致病菌*Erysiphe necator* [synonym *Uncinula necator* (Schw.) Burr.]引起的真菌性病害,可引起叶片褪绿,覆盖白色粉层进而导致叶片卷曲、枯萎等症状。同葡萄霜霉病一样,葡萄白粉病抗性位点较多(表3),命名为Run(Resistance to *Uncinula necator*)或Ren(Resistance to *Erysiphe necator*)。Barker等[59]首次将抗白粉病Run1定位在圆叶葡萄的12号染色体上,而欧亚种不携带该基因。目前以圆叶葡萄和欧亚种葡萄的BC_5为材料,已经获得与Run1基因连锁的分子标记[60]。Hoffmann等[53]将Ren1抗性位点定位于Nimrang的LG13上的VMC9H4-2、VMCNG4E10-1和UDV-020附近,该区域包含多个NBS-LRR基因。在中国野生群体利用中,Pap等[35]在中国野生葡萄变叶葡萄*V. piasezkii*(Dvit2027)中发现了2个抗白粉病的QTL位点Ren6和Ren7,分别位于第9和第19染色体上。目前白粉病抗性位点在2(Ren10)、9(Ren6)、12(Run1)、13(Ren1)、14(Ren2,Ren5)、15(Ren3,Ren9)、18(Run2.1、Run2.2、Ren4、Ren8)、19(Ren7)号染色体上鉴定出来(表3)解释的表型变异率从14%到76%。

表3 白粉病抗性位点

Table 3 Downy mildew resistance site

位点 Locus	亲本 Parents	染色体 Chromosome	位置 Position/Mb	紧密连锁标记 Associated marker	表型变异率 Phenotypic variance/%	参考文献 Reference
Ren1	Nimrang×Kishmish Vatkana	13	18.4	VMC9h4-2	–	[53]
Ren2	Horizon×Illinois 547-1	14	26.9	CS25	76.0	[54]
Ren3	Regent×Red Globe	15	4.9	VChr15CenGen02	43.9	[16]
Ren4	C166-043×F8909-08	18	26.9	VMC7f2	70.0	[55]
Ren5	Regale×Regale	14	4.8	VMC9c1	58.0	[56]
Ren6	F2-35×V. Piasezkii (Dvit2027)	9	8.6	PN9-057	62.0	[35]
Ren7	F2-35×V. Piasezkii (Dvit2027)	19	0.2	VVIp17.1	18.1	[35]
Ren8	GF.GA-47-42×Villard Blanc	16	13.2	UDV117	14.0	[36]
Ren9	Regent×Lemberger	15	1.4	CenGen6	46.2	[57]
Ren10	MN1264×MN1214	2	17.9	S2_17 854 965	13.3	[58]
Run1	VRH3082-1-42×Cabernet Sauvignon	12	13.1	VMC4f3.1	–	[59]
Run2.1	A90-71×Flame Seedless	18	26.9	VMC7f2	52.8	[55]
Run2.2	e2-9×Malaga Rosada	18	26.9	VMC7f2	50.0	[55]

2.3 其他病害抗性QTL定位

其他葡萄病害,如皮尔斯病、冠瘿病、黑腐病、炭疽病、白腐病等,对葡萄也有较大危害,但QTL定位研究相对较少。在抗皮尔斯病的QTL研究中,Krivanek等[61]首先将抗皮尔斯病Pdr1(Pierces disease resistance 1)定位于14号染色体上;随后Riaz等[62]通过精细定位将抗皮尔斯病的主效QTL定位到14号染色体VVIn64和UDV095标记附近。在抗冠瘿病QTL定位方面,Kuczmog等[63]将Rcg1(Resistance to Crown gall 1)定位在抗冠瘿病亲本Kunbarát(*V. amurensis*)的15号染色体上,紧密连锁标记9M3-3距Rcg1位点576 kb远。关于黑腐病QTL研究较少,Rex等[34]将黑腐病2个抗性位点Rgb1(Resistance to *Guignardia bidwellii* 1)和Rgb2分别定位在14号和16号染色体上。近年来,部分科技人员对葡萄抗炭疽病进行QTL定位,高晓铭等[64]利用里扎马特×黑珍珠杂交F_1代群体,在12号染色体检测到解释表型变异率37.07%、贡献率为71.50%的抗炭疽病主效QTL。Fu等[40]对Cabernet Sauvignon × Shuang Hong杂交群体进行了连续3年抗炭疽病鉴定,在14号染色体发现抗性位点Rgr1(Resistance to *Colletotrichum* 1),此区间包含了11个NBS-LRR基

因。2021年，Su等[19]利用Zhuosexiang × Victoria杂交群体在14号染色体上定位到一个抗葡萄白腐病QTL，并预测了7个可能抗白腐病的候选基因。这些定位结果为分子标记在育种中的使用奠定了基础。

3　问题及展望

构建遗传图谱和开发目标性状紧密连锁的分子标记，对MAS育种效率的提升具有重要意义。近年来，葡萄遗传图谱的构建发展较快，获得一些成果，但仍存在问题。许多葡萄遗传图谱使用RFLP、AFLP、RAPD、SSR等第一代和第二代标记构建，导致图谱标记密度较低，各连锁群标记间距较大，标记在基因组分布不均匀，无法有效定位候选基因。随着测序技术的发展，SNP标记已经用来构建高密度遗传图谱，提高了图谱的饱和度并显著提高精细定位程度。但SNP在不同种群间通用性较低[6]，在将来应考虑构建多种标记整合的图谱，提高图谱的饱和性与通用性。分子标记辅助选择是将分子标记应用于葡萄品种改良过程中进行选择的一种辅助手段，主要包括对目标性状的前景选择和对遗传背景的背景选择。目前葡萄分子标记辅助育种仍以SSR标记为主，但SSR分子标记通性低、费时，而SNP标记适合高通量、自动化检测，可能成为未来首选的标记系统[6]。然而SNP分子标记在葡萄MAS中的实际应用仍然较少[37,65]，因此应加大对性状关联SNP标记的转化和应用。

葡萄抗病性作为一个复杂的数量性状，受到较多基因的调控，且基因之间还存在着互作效应，遗传机制非常复杂。虽然已有许多针对抗病性状的QTL定位研究，但由于抗病性状往往受到多个QTL控制，且影响群体QTL检测的因素很多，如环境因素、群体大小及分子标记连锁图谱的饱和度等[6]。另外葡萄定位常使用群体数量较小的初级作图群体F_1，容易造成定位误差。因此，将来在研究中应构建群体数量较大的F_2、BC（回交群体）等群体，消除遗传背景对QTL定位产生的不利影响[9]，提高QTL检测灵敏度和定位精度。随后通过这些位点解析抗病性状的遗传和分子机制，挖掘葡萄抗病优良基因，为葡萄抗病育种奠定基础。另外葡萄抗病定位研究主要集中在霜霉病和白粉病，而对我国危害较大的灰霉病和黑痘病尚未见报道，应加大对这些病害的解析。

葡萄多个图谱以及病害抗性QTL位点已经发表，但这些实验数据（基因型、表型）和位点信息未储存在公共数据库，极大限制了图谱的整合以及定位信息的有效利用。作为模式作物水稻，其表型和图谱信息以及QTL相关数据可以在Gramene数据库进行检索，促进了QTL位点利用和候选基因的挖掘[66]。因此未来应构建可以共享的葡萄的QTL定位数据库，以提高QTL数据的利用与挖掘。

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