DOI: 10.3724/SP.J.1006.2021.04099

马铃薯资源晚疫病抗性的全基因组关联分析

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摘要: 广谱抗性基因的挖掘是马铃薯高抗晚疫病品种选育的基础。本研究以 288 份国际马铃薯中心筛选的晚疫病抗性群体为试验材料, 经过连续 2 年田间调查, 计算 AUDPC 和 sAUDPC 值, 评估群体晚疫病抗性; 利用 SLAF-seq 方法进行群体简化基因组测序, 通过对晚疫病抗性表型数据的全基因组关联分析, 挖掘晚疫病抗性相关的遗传位点和候选基因, 为晚疫病抗性品种选育和抗病机理研究提供一定的理论和材料基础。结果表明, 晚疫病抗性在 288 份材料间存在着广泛的遗传差异; 基于 5 种分析模型, 共鉴定到 82 个与晚疫病抗性显著关联的位点; 在关联区间关联到 54 个已知或可能与晚疫病抗性相关的基因。其中, 23 个基因为抗性基因, 包括晚疫病抗性基因 *R1* 同源基因、*Sw-5* 同源基因(*R8*)和 *Rpi-vnt1* 以及编码多效性耐药蛋白基因; 5 个基因编码 MAPK 蛋白和 WRKY 转录因子; 1 个基因参与茉莉酸途径; 3 个基因与水杨酸途径相关; 6 个基因是病程相关的基因; 3 个基因参与苯基丙酸类合成途径; 其他与晚疫病抗性相关的基因, 如 HMGR 基因(2 个)、细胞色素 P450 (21 个)。

关键词: 马铃薯; 晚疫病抗性; 全基因组关联分析; 抗性基因; 国际马铃薯中心

Genome-wide association analysis for late blight resistance of potato resources

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Abstract: The mining of broad-spectrum resistance genes is the basis of the breeding of potato varieties with high late blight resistance. In this study, 288 samples of late disease resistance selected by the International Potato Center (CIP) for years were planted and were investigated for two consecutive years, which could provide some theoretical and material basis for breeding of late blight resistant varieties and help to study on disease resistance mechanism. The late blight resistance of each sample was evaluated using AUDPC and sAUDPC values. The population simplified genome sequencing was performed by SLAF-seq and carried out by genome-wide association analysis in order to discover the genetic loci and candidate genes related to late blight resistance. There were wide genetic differences in resistance to late blight among 288 samples. Through genome-wide association analysis, based on five analytical models, a total of 82 loci significantly correlated with late blight resistance were identified. Combined with genomic annotation, there were 54 candidate genes known or likely to be associated with late blight resistance in the association interval. Among them, 23 genes were resistant genes, including late blight resistance gene *R1* homolog, *Sw-5* homolog (*R8*) and *Rpi-vnt1*, as well as gene encoding pleiotropic resistance protein. Five genes encoded MAPK protein and WRKY transcription factor; one gene was involved in the JA pathway; three genes were associated with salicylic acid pathway; six genes were related to the course of the disease; three genes were involved in the synthesis of phenylpropionic acid. Other genes related

本研究由国家自然科学基金项目(31760409, 31460368), 云南省农业联合重点项目[2017FG001(-012)]和国际马铃薯中心合作项目 TON (14.1432.5-001.00)资助。

This study was supported by the National Natural Science Foundation of China (31760409, 31460368), the Yunnan Agricultural Foundation Projects [2017FG001 (-012)], and the International Potato Center Collaboration Program TON (14.1432.5-001.00).

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Received (收稿日期): 2020-04-30; Accepted (接受日期): 2020-09-13; Published online (网络出版日期): 2020-09-28.

URL: <https://kns.cnki.net/kcms/detail/11.1809.S.20200927.1805.004.html>

to resistance to late blight included HMGR gene (2) and cytochrome P450 (21).

Keywords: potato; late blight resistance; genome-wide association analysis; resistance gene; CIP

晚疫病是马铃薯的主要病害, 每年可造成我国马铃薯减产约 10%~15%, 经济损失高达 20 亿美元。西南地区低温高湿的气候环境, 晚疫病发生更严重, 马铃薯减产可达 15%~40%^[1-2]。提高品种晚疫病抗性是马铃薯育种重要目标之一, 而挖掘持久、高抗的晚疫病抗性基因对马铃薯抗病育种具有重要的意义。

20 世纪 50 年代, 育种家将野生种 *Solanum demissum* 的抗性基因导入到栽培种中, 但抗性很快被新出现的晚疫生理小种克服^[3-4]。目前已经鉴定并克隆到一些对晚疫病表现出广谱抗性的 *R* 基因。通过构建 BAC 文库和长片段 PCR 扩增的方法, 从野生种 *S. bulbocastanum* 中克隆了第 1 个马铃薯晚疫病广谱抗性基因 *RB* 或 *Rpi-blb1*^[5-6]。通过构建 *S. bulbocastanum* 作图群体, 利用 AFLP 分子标记, 克隆到另 1 个广谱抗性基因 *Rpi-blb2*^[4]。利用野生种 *S. venturii* 的 5 个作图群体, 结合分离群体分组分析法(bulked segregant analysis, BSA)找到与抗性基因连锁的 AFLP 分子标记, 通过构建 BAC 文库从而克隆了广谱抗性基因 *Rpi-vnt1*^[7]。对含有广谱抗性基因 *R8* 分子标记或 QTL 位点的群体构建 BAC 文库, 通过酶切 PCR 克隆到了该基因^[8-9]。上述这些基因的鉴定主要是通过构建遗传群体、分子标记定位获得, 而通过自然群体全基因组关联分析定位晚疫病抗性基因的研究较少。

本研究选择的自然群体引自国际马铃薯中心, 该中心从 19 世纪 80 年代起以淘汰马铃薯晚疫病垂直抗性而保留其水平抗性为目的, 筛选了一批群体材料。因此, 该群体中很可能保留着晚疫病广谱抗性基因。通过对四倍体马铃薯群体连续 2 年的田间晚疫病抗性评价, 结合群体简化基因组测序获得大量的 SNP 位点, 进行全基因组关联分析挖掘晚疫病抗性相关的遗传位点和候选基因, 旨在为晚疫病抗性品种选育和抗病机理研究提供一定的理论和材料基础。

1 材料与方法

1.1 材料

引自国际马铃薯中心的 288 份四倍体马铃薯晚疫病抗性群体材料(表 1), 感病对照为 Desiree (D214)。群体 A 中晚疫病抗性来源为改良的 *S. demissum* 衍生抗

性, 包括来自安第斯栽培种 *S. tuberosum* groups *andigena*、*phureja* 和 *stenotomum*, 以及野生种 *S. acaule* 和 *S. bulbocastanum* 抗性的材料 8 份; 群体 B3 来源于群体 A, 但筛选保留表现出晚疫病水平抗性的资源材料 82 份; 群体 B1 来自 *S. tuberosum* groups *andigena* 的材料 15 份; 群体 LTVR 具有马铃薯病毒病(PVY、PVX 和 PLRV)抗性、生长期短和适应温暖环境特性的材料 111 份; 群体 B3-HT 结合群体 B3 的晚疫病抗性、北美和欧洲品种的耐热性以及群体 LTVR 特性的材料 34 份; 群体 B3-LTVR 包括群体 B3 和群体 LTVR 的杂交后代 22 份; 群体 BW 具有细菌性枯萎病抗性的材料 12 份; 群体 PREBRED 具有从野生种导入到四倍体 B3 或 LTVR 中的晚疫病抗性材料 1 份; VARIETY 表示马铃薯品种 3 份^[10]。

1.2 田间试验和表型数据分析

2015—2016 年, 群体材料种植于云南省曲靖市会泽县试验基地(26°06'N, 103°22'E), 海拔 2650 m。每个材料种植 1 行 10 株, 行距为 0.7 m, 株距为 0.3 m, 种植 3 次重复。采用 Alpha 试验设计(CIP 提供软件), 整个生长季进行正常中耕、施肥管理等, 但不喷洒杀菌类农药。

调查田间晚疫病发病比率。发现初始病株, 每 7 d 调查 1 次, 共调查 8 次, 计算 AUDPC 和 sAUDPC 值。利用 Microsoft Excel 对所观测到的数据进行统计分析。

$$\text{AUDPC} = \sum_{i=1}^{n-1} \left[\frac{(x_{i+1} + x_i)}{2} \right] (t_{i+1} - t_i)$$

$$\text{sAUDPC} = \text{AUDPC}_{\text{评估材料}} / \text{AUDPC}_{\text{感病对照}}^{*9}$$

式中, n 表示总的调查次数, x_i 表示第 i 次调查的晚疫病严重程度, t_i 表示第 i 次调查的时间。

1.3 DNA 提取和测序方法

利用 CTAB 法提取 DNA, 检测合格后利用 Illumina HiSeq2500 测序仪(Illumina, Inc; San Diego, CA, USA)测序。以马铃薯 *S. chacoense* M6 的基因组测序信息为参考^[11], 利用北京百迈客生物有限公司自主研发的简化基因组测序流程 SLAF-seq^[12]进行电子酶切预测, 根据最佳酶切方案选择 *Rsa* I+*Hae* III 进行酶切, 酶切长度在 314~414 的序列被定义为 SLAF 标签, 获得多态性标签 1,032,778 个。以马铃

薯 *S. chacoense* M6 为参考基因组, 利用 BWA 软件^[13]将 reads 比对到参考基因组上, 利用 GATK^[14]和 SAMtools^[15]软件筛选 SNP。根据完整度大于 0.8, 次要基因频率大于 0.05 过滤后, 得到 353,753 个 SNP 位点进行后续的分析。

1.4 晚疫病抗性全基因组关联分析

基于 SNP 位点, 利用 TASSEL 软件^[16]的混合线性模型(compressed mixed linear model, CMLM), 通过公式 $y = X\alpha + Q\beta + K\mu + e$ 得到关联值。公式中, 通过 Admixture 软件^[17]计算样品群体结构 Q 矩阵, SPAGeDi 软件^[18]计算样品间亲缘关系 K 矩阵, X 为基因型矩阵, y 为表型, 最终获得每个 SNP 位点的关联值, 并计算它们的 P 值。以 AUDPC_2015、AUDPC_2016、sAUDPC_2015、sAUDPC_2016, 以

及这 2 年的 AUDPC 和 sAUDPC 平均值即 AUDPC_Mean 和 sAUDPC_Mean 为表型数据, 共分析 6 个性状。对这些性状利用 GLM、MLM、CMLM、FASTLMM 和 EMMAX 五种模型进行关联分析。利用 GGplot2 软件^[19]绘制 Quantile-Quantile 散点图(Q-Qplot), 利用 QQman 软件绘制曼哈顿图(Manhattan), 展示关联分析显著的 SNP 位点。

1.5 候选基因预测

对 6 个性状在 5 种模型下获得的显著水平是 0.1 和 0.01 的关联 SNP 位点进行注释。选取这些位点前后 100 kb 范围内的基因, 利用 BLAST 软件分别与 NR、SwissProt、GO、COG 和 KEGG 数据库进行比对, 获得关联区域内基因注释信息, 并根据注释信息寻找与晚疫病抗性相关的候选基因。

表 1 自国际马铃薯中心引进的 288 份马铃薯群体材料
Table 1 288 potato population resources from CIP

编号 Code	CIP 编号 CIP accession	群体 Population	编号 Code	CIP 编号 CIP accession	群体 Population	编号 Code	CIP 编号 CIP accession	群体 Population
C001	CIP381381.13	A	C106	CIP392740.4	LTVR	D095	CIP394900.1	BW
C002	CIP391065.69	B3	C107	CIP392745.7	LTVR	D096	CIP395011.2	B3
C003	CIP391583.25	B3	C108	CIP392759.1	LTVR	D097	CIP395015.6	B3
C004	CIP392617.54	B3	C109	CIP393613.2	LTVR	D098	CIP395017.14	B3
C005	CIP392634.52	B3	C110	CIP393615.6	LTVR	D099	CIP395017.227	B3
C006	CIP393073.179	B3	C112	CIP397030.31	LTVR	D100	CIP395017.229	B3
C007	CIP393073.197	B3	C113	CIP397035.26	LTVR	D101	CIP395017.242	B3
C008	CIP393227.66	B3	C114	CIP302428.20	LTVR	D102	CIP395037.107	B3
C009	CIP393228.67	B3	C115	CIP302476.108	LTVR	D103	CIP395077.12	B3
C010	CIP393371.164	B3	C116	CIP302499.30	LTVR	D105	CIP395096.2	B3
C011	CIP391004.18	B3	C117	CIP304345.102	LTVR	D106	CIP395109.29	B3
C012	CIP392657.171	B3	C118	CIP304350.100	LTVR	D107	CIP395109.34	B3
C013	CIP393280.64	B3	C119	CIP304350.118	LTVR	D108	CIP395111.13	B3
C014	CIP391047.34	B3	C120	CIP304350.95	LTVR	D109	CIP395112.19	B3
C015	CIP391058.175	B3	C121	CIP304371.67	LTVR	D110	CIP395112.32	B3
C016	CIP393085.5	B3	C122	CIP304383.41	LTVR	D111	CIP395112.36	B3
C017	CIP398192.213	B3-HT	C123	CIP304383.80	LTVR	D112	CIP395112.6	B3
C018	CIP398098.119	B3-HT	C124	CIP304387.39	LTVR	D113	CIP395123.6	B3
C019	CIP398098.203	B3-HT	C125	CIP304405.47	LTVR	D114	CIP395169.17	B3
C020	CIP398180.253	B3-HT	C127	CIP397077.16	LTVR	D117	CIP395448.1	BW
C021	CIP398180.289	B3-HT	C128	CIP391919.3	BW	D118	CIP396004.225	B3
C024	CIP398193.553	B3-HT	C129	CIP391930.1	BW	D119	CIP396004.263	B3
C025	CIP398203.509	B3-HT	C130	CIP391931.1	BW	D121	CIP396008.104	B3
C026	CIP398208.219	B3-HT	C131	CIP394906.6	BW	D123	CIP396009.258	B3
C027	CIP398208.33	B3-HT	C132	CIP395438.1	BW	D124	CIP396012.266	B3
C028	CIP398208.58	B3-HT	C133	CIP394904.20	BW	D126	CIP396023.109	B3
C029	CIP398208.704	B3-HT	D001	CIP300055.32	LTVR	D127	CIP396026.101	B3

(续表 1)

编号 Code	CIP 编号 CIP accession	群体 Population	编号 Code	CIP 编号 CIP accession	群体 Population	编号 Code	CIP 编号 CIP accession	群体 Population
C030	CIP301024.14	B3-LTVR	D002	CIP300063.9	LTVR	D128	CIP396026.103	B3
C031	CIP301029.18	B3-LTVR	D003	CIP300065.4	LTVR	D130	CIP396031.108	B3
C032	CIP301040.63	B3-LTVR	D005	CIP300135.3	LTVR	D131	CIP396031.119	B3
C033	CIP300046.22	LTVR	D007	CIP301023.15	B3-LTVR	D132	CIP396033.102	B3
C034	CIP300048.12	LTVR	D008	CIP301024.95	B3-LTVR	D133	CIP396034.103	B3
C035	CIP300054.29	LTVR	D009	CIP301026.23	B3-LTVR	D134	CIP396034.268	B3
C036	CIP300056.33	LTVR	D011	CIP301041.26	B3-LTVR	D137	CIP396038.101	B3
C037	CIP300063.4	LTVR	D012	CIP301044.36	B3-LTVR	D138	CIP396038.105	B3
C038	CIP300066.11	LTVR	D013	CIP301045.74	B3-LTVR	D139	CIP396038.107	B3
C039	CIP300072.1	LTVR	D014	CIP301055.53	B3-LTVR	D140	CIP396043.226	B3
C040	CIP300093.14	LTVR	D015	CIP301056.54	B3-LTVR	D142	CIP396063.1	B3-LTVR
C041	CIP300099.22	LTVR	D017	CIP303381.106	LTVR	D143	CIP396063.16	B3-LTVR
C042	CIP300101.11	LTVR	D018	CIP303381.30	LTVR	D144	CIP396180.22	B3-LTVR
C043	CIP379706.27	LTVR	D019	CIP304347.6	LTVR	D145	CIP396240.2	B3
C044	CIP385499.11	LTVR	D021	CIP304350.18	LTVR	D147	CIP396241.4	B3
C046	CIP388676.1	LTVR	D022	CIP304350.78	LTVR	D148	CIP396244.12	B3
C047	CIP388972.22	LTVR	D023	CIP304351.109	LTVR	D149	CIP396268.1	B3-LTVR
C048	CIP390478.9	LTVR	D024	CIP304351.31	LTVR	D150	CIP396268.9	B3-LTVR
C049	CIP391207.2	LTVR	D025	CIP304366.46	LTVR	D151	CIP396269.14	B3-LTVR
C050	CIP391382.18	LTVR	D028	CIP304371.58	LTVR	D152	CIP396269.16	B3-LTVR
C051	CIP392781.1	LTVR	D029	CIP304387.17	LTVR	D154	CIP396272.18	B3-LTVR
C052	CIP392797.22	LTVR	D030	CIP304387.92	LTVR	D156	CIP396272.21	B3-LTVR
C053	CIP392822.3	LTVR	D031	CIP304394.56	LTVR	D157	CIP396272.37	B3-LTVR
C054	CIP392973.48	LTVR	D033	CIP304399.5	LTVR	D158	CIP396273.48	B3-LTVR
C056	CIP394034.65	LTVR	D035	CIP304406.31	LTVR	D160	CIP397006.18	LTVR
C057	CIP394034.7	LTVR	D036	CIP374080.5	A	D162	CIP397039.53	LTVR
C058	CIP394579.36	LTVR	D037	CIP377744.1	A	D164	CIP397060.19	LTVR
C059	CIP394600.52	LTVR	D040	CIP381178.14	A	D165	CIP398098.205	B3-HT
C061	CIP394613.139	LTVR	D041	CIP381379.12	A	D166	CIP398098.231	B3-HT
C062	CIP394613.32	LTVR	D042	CIP381381.9	A	D167	CIP398098.570	B3-HT
C063	CIP394614.117	LTVR	D043	CIP381403.16	A	D168	CIP398098.65	B3-HT
C064	CIP394881.8	LTVR	D044	CIP384321.3	A	D169	CIP398180.144	B3-HT
C065	CIP395186.6	LTVR	D047	CIP387164.4	B3	D170	CIP398190.112	B3-HT
C066	CIP395193.6	LTVR	D048	CIP389746.2	B3	D171	CIP398190.200	B3-HT
C067	CIP395195.7	LTVR	D050	CIP391011.17	B3	D172	CIP398190.404	B3-HT
C068	CIP395196.4	LTVR	D051	CIP391046.14	B3	D173	CIP398190.523	B3-HT
C069	CIP395197.5	LTVR	D052	CIP391065.81	B3	D174	CIP398190.530	B3-HT
C070	CIP395432.51	LTVR	D053	CIP391580.30	B3	D175	CIP398190.571	B3-HT
C071	CIP395434.1	LTVR	D054	CIP391585.179	B3	D176	CIP398190.605	B3-HT
C072	CIP395436.8	LTVR	D055	CIP391585.5	B3	D177	CIP398190.615	B3-HT
C076	CIP397012.22	LTVR	D057	CIP392025.7	LTVR	D178	CIP398190.735	B3-HT
C078	CIP397016.7	LTVR	D058	CIP392285.72	BW	D179	CIP398192.41	B3-HT
C079	CIP397029.21	LTVR	D059	CIP392633.64	B3	D180	CIP398192.553	B3-HT
C080	CIP397036.7	LTVR	D060	CIP392634.49	B3	D181	CIP398192.592	B3-HT
C081	CIP397039.51	LTVR	D061	CIP392637.10	B3	D182	CIP398193.158	B3-HT

(续表 1)

编号	CIP 编号	群体	编号	CIP 编号	群体	编号	CIP 编号	群体
Code	CIP accession	Population	Code	CIP accession	Population	Code	CIP accession	Population
C082	CIP397044.25	LTVR	D064	CIP392821.1	LTVR	D183	CIP398193.650	B3-HT
C083	CIP397055.2	LTVR	D065	CIP393075.54	B3	D185	CIP398208.29	B3-HT
C084	CIP397065.2	LTVR	D067	CIP393077.54	B3	D186	CIP398208.505	B3-HT
C085	CIP397067.2	LTVR	D068	CIP393079.24	B3	D187	CIP398208.620	B3-HT
C086	CIP397069.5	LTVR	D069	CIP393079.4	B3	D188	CIP398208.670	B3-HT
C087	CIP397073.15	LTVR	D070	CIP393083.2	B3	D189	CIP399001.44	B1
C088	CIP397078.12	LTVR	D071	CIP393084.31	B3	D190	CIP399004.19	B1
C089	CIP397079.26	LTVR	D072	CIP393220.54	B3	D192	CIP399049.14	B1
C090	CIP397079.6	LTVR	D074	CIP393248.55	B3	D193	CIP399049.16	B1
C091	CIP397098.12	LTVR	D075	CIP393280.57	B3	D194	CIP399049.22	B1
C092	CIP397099.6	LTVR	D077	CIP393284.39	B3	D195	CIP399053.11	B1
C093	CIP397100.9	LTVR	D078	CIP393339.242	B3	D196	CIP399053.15	B1
C094	CIP397196.3	LTVR	D079	CIP393349.68	B3	D199	CIP399067.22	B1
C095	CIP397196.8	LTVR	D080	CIP393371.157	B3	D201	CIP399072.28	B1
C096	CIP397197.9	LTVR	D081	CIP393371.159	B3	D203	CIP399075.32	B1
C097	CIP398014.2	LTVR	D082	CIP393371.58	B3	D205	CIP399078.11	B1
C098	CIP388611.22	LTVR	D083	CIP393382.44	B3	D206	CIP399079.22	B1
C099	CIP388615.22	LTVR	D084	CIP393385.39	B3	D207	CIP399083.4	B1
C100	CIP389468.3	LTVR	D085	CIP393385.47	B3	D209	CIP399085.23	B1
C101	CIP390637.1	LTVR	D088	CIP393617.1	LTVR	D210	CIP399085.30	B1
C102	CIP391180.6	LTVR	D089	CIP394223.19	LTVR	D212	CIP694474.33	PREBRED
C103	CIP391533.1	LTVR	D092	CIP394895.7	BW	D214	CIP800048	VARIETY
C104	CIP391724.1	LTVR	D093	CIP394898.13	BW	D216	CIP800923	VARIETY
C105	CIP392032.2	LTVR	D094	CIP394899.5	BW	D217	CIP800959	VARIETY

群体 A 中晚疫病抗性来源为改良的 *S. demissum* 衍生抗性; 群体 B3 来源于群体 A, 筛选保留表现出晚疫病水平抗性的资源; 群体 B1 来自 *S. tuberosum* groups *andigena* 的抗性材料; 群体 LTVR 具有马铃薯病毒病(PVY、PVX 和 PLRV)抗性、生长期短和适应温暖环境特性的材料; 群体 B3-HT 结合群体 B3 的晚疫病抗性、北美和欧洲品种的耐热性以及群体 LTVR 特性的材料; 群体 B3-LTVR 包括群体 B3 和群体 LTVR 的杂交后代; 群体 BW 具有细菌性枯萎病抗性的材料; 群体 PREBRED 具有从野生种导入到四倍体 B3 或 LTVR 中的晚疫病抗性材料; VARIETY 表示马铃薯品种。

The late blight resistance of population A was resource from *S. demissum*-derived; population B3 was derived from population A, and resources showing late blight resistance were screened and retained; population B1 was derived from the resistant material of *S. tuberosum* groups *andigena*; population LTVR were resistant to potato virus disease (PVY, PVX, and PLRV), and had a short growth period and adapted to warm climate; the population B3-HT included late blight resistance from population B3, the heat resistance of North American and European varieties, and the properties of population LTRV; population B3-LTVR included hybrid offsprings of population B3 and LTVR; population BW had bacterial wilt resistance; the PREBRED had late blight resistance imported from wild species to tetraploid B3 or LTVR; VARIETY represented potato varieties.

2 结果与分析

2.1 晚疫病抗性的表型分析

通过对 288 份马铃薯资源材料连续 2 年的晚疫病田间抗性评价发现, 晚疫病抗性评价价值 AUDPC 和 sAUDPC 呈连续分布。2015 年所有材料的 AUDPC 平均值为 2244.1, 范围是 121.3~4740.8, 变异系数为 61.73%, sAUDPC 平均值为 3.9, 范围是 0.2~8.3, 变异系数为 61.56%; 2016 年所有材料的

AUDPC 平均值为 1228.5, 范围是 72.7~3371.3, 变异系数为 80.47%, sAUDPC 平均值为 3.6, 范围是 0.2~9.5, 变异系数为 80.21%。表明该群体表现出晚疫病抗性广泛的遗传差异, 且受多基因控制, 属于数量性状遗传。相关性分析中, 2015—2016 年 AUDPC 值相关系数为 0.8988, 高度线性相关; sAUDPC 值相关系数为 0.8974, 高度线性相关(图 1)。表明 2 年间群体材料田间晚疫病抗性表现一致, 抗性稳定。

图 1 288 份群体材料 AUDPC 和 sAUDPC 频次分布图及相关性散图(2015–2016 年)

Fig. 1 Frequency distribution and correlation of the AUDPC and sAUDPC values of 288 samples in 2015 and 2016

A: 2015 年 AUDPC 值; B: 2016 年 AUDPC 值; C: 2015 年 sAUDPC 值; D: 2016 年 sAUDPC 值; E: 2015 年和 2016 年 AUDPC 值相关性散布图; F: 2015 年和 2016 年 sAUDPC 值相关性散布图。

A: AUDPC value in 2015; B: AUDPC value in 2016; C: sAUDPC in 2015; D: sAUDPC in 2016; E: correlation plots of AUDPC values between 2015 and 2016; F: correlation plots of sAUDPC values between 2015 and 2016.

2.2 马铃薯晚疫病抗性的全基因组关联分析

5 种模型下对 6 个性状分析的 QQ 图结果表明, 在所有模型下关联到显著相关的 SNP 位点都是可靠的(图 2 是 2 个性状 AUDPC_mean 和 sAUDPC_mean 在 5 种模型下的 QQ 图)。在 5 种分析模型下, 共关联到与 6 种晚疫病抗性性状显著相关(显著水平为 0.1 和 0.01)的 SNP 位点 82 个(表 2 和图 3)。其中, 6 个 SNP 位点分布在 3 号染色体(图 3-A, B); 3 个 SNP 位点分布在 4 号染色体(图 3-A, B); 1 个 SNP 位点分布在 5 号染色体(图 3-B, C); 分别有 2 个 SNP 位点分布在 6 号、7 号染色体(图 3-A, B, D); 66 个 SNP 位点分布在 9 号染色体(图 3-A~D); 各有 1 个 SNP 位点分布在 11 号和 12 号染色体(图 3-A, B, D)。在 82 个 SNP 位点中, 20 个 SNP 位点在所有模型分析中, 2 种显著水平情况下, 与所有性状都相关。它们是 31,375,673 (第 9 个)、31,707,832 (第 23 个)、32,382,888 (第 25 个)、32,973,114 (第 35 个)、33,118,463 (第 36 个)、33,145,927 (第 38

个)、33,148,740 (第 39 个)、33,156,262 (第 40 个)、33,211,574 (第 43 个)、33,244,698 (第 48 个)、33,283,731 (第 49 个)、33,283,949 (第 50 个)、33,451,096 (第 53 个)、33,480,937 (第 55 个)、34,959,324 (第 62 个)、35,060,347 (第 66 个)、35,065,836 (第 67 个)、35,123,523 (第 72 个)、35,212,534 (第 77 个)、35,256,410 (第 80 个)。同一性状下, GLM 模型分析定位到的 SNP 位点数目最多, 而 MLM 模型分析定位到的 SNP 位点数目最少。在 GLM 模型下分析, 显著水平为 0.1 时定位到与 AUDPC_Mean 相关的 SNP 位点数目(74 个)最多(表 2)。

2.3 候选基因预测

本研究在 82 个关联 SNP 位点上下游区域 100 kb, 共检测到 922 个候选基因。其中, 460 个候选基因在所有分析(60 种)中都存在, 其余基因在 2~56 种分析中出现。根据基因组注释, 筛选出 54 个已知或可能与晚疫病抗性相关的基因(表 3)。其中, 23 个基因为抗性基因包括晚疫病抗性基因 *R1* 同源基因、*Sw-5*

图 2 AUDPC_mean (A: CMLM; C: EMMAX; E: FASTLMM; G: GLM; I: MLM 模型)和 sAUDPC_mean (B: CMLM; D: EMMAX; F: FASTLMM; H: GLM; J: MLM 模型)不同模型下的 QQ 图

Fig. 2 QQ plots of AUDPC_mean and sAUDPC_mean under different analytical model (AUDPC A: CMLM; C: EMMAX; E: FASTLMM; G: GLM; I: MLM; sAUDPC B: CMLM; D: EMMAX; F: FASTLMM; H: GLM; J: MLM)

表 2 6 个马铃薯晚疫病抗性性状在不同分析模型和显著水平下的显著关联标记

Table 2 Significant correlation markers of six phenotype of potato resistance to late blight under different analytical models and significant levels

编号 Number	SNP 位点 SNP locus	染色体 Chr.	不同模型、显著水平下与 SNP 相关联的性状 Traits correlated with SNP under different analytical models and significant level
1	10774833	3	5 ^d _0.1, 6 ^d _0.1
2	10774840	3	5 ^d _0.1
3	10774841	3	5 ^d _0.1
4	14767856	3	3 ^d _0.1, 4 ^d _0.1, 6 ^d _0.1
5	18132045	3	3 ^d _0.1, 4 ^d _0.1
6	32015964	3	3 ^d _0.1, 4 ^d _0.1, 6 ^d _0.1
7	7144093	4	5 ^d _0.1, 6 ^d _0.1
8	17868575	4	3 ^d _0.1, 4 ^d _0.1
9	31375673	4	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d, e_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.01, 3 ^a , b, c, d, e_0.1, 3 ^a , b, c, d, e_0.01, 4 ^a , b, c, d, e_0.1, 4 ^a , b, c, d, e_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d, e_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.01
10	4579130	5	3 ^b , c, d_0.1, 3 ^b , c_0.01, 4 ^b , c, d_0.1, 4 ^b _0.01
11	2241058	6	1 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.1, 1 ^b , c, d_0.01, 2 ^b , c, d_0.01, 3 ^d _0.1, 4 ^d _0.1, 3 ^d _0.01, 4 ^d _0.01, 5 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.1, 5 ^d _0.01, 6 ^d _0.01
12	2241060	6	1 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.1, 1 ^b , c, d_0.01, 2 ^b , c, d_0.01, 3 ^d _0.1, 4 ^d _0.1, 3 ^d _0.01, 4 ^d _0.01, 5 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.1, 5 ^d _0.01, 6 ^d _0.01
13	17610976	7	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1, 5 ^d _0.01
14	37485429	7	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
15	22968094	9	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
16	30491004	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
17	30518418	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
18	30522602	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
19	30542106	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
20	30550212	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
21	30568973	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
22	31001787	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
23	31707832	9	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d, e_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.01, 3 ^a , b, c, d, e_0.1, 3 ^a , b, c, d, e_0.01, 4 ^a , b, c, d, e_0.1, 4 ^a , b, c, d, e_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d, e_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.01
24	32170544	9	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
25	32382888	9	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d, e_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.01, 3 ^a , b, c, d, e_0.1, 3 ^a , b, c, d, e_0.01, 4 ^a , b, c, d, e_0.1, 4 ^a , b, c, d, e_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d, e_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.01
26	32442672	9	1 ^d _0.1
27	32468577	9	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d, e_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.01, 3 ^a , b, c, d, e_0.1, 3 ^a , b, c, d, e_0.01, 4 ^a , b, c, d, e_0.1, 4 ^a , b, c, d, e_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d, e_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.01
28	32627854	9	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d_0.01, 3 ^a , b, c, d_0.1, 3 ^a , b, c, d_0.01, 4 ^a , b, c, d_0.1, 4 ^a , b, c, d_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d_0.01
29	32642867	9	1 ^a , c, d, e_0.1, 2 ^a , c, d, e_0.1, 1 ^d _0.01, 2 ^d _0.01, 3 ^d _0.1, 4 ^d _0.1, 3 ^d _0.01, 4 ^d _0.01, 5 ^a , d, e_0.1, 6 ^a , d, e_0.1, 5 ^a , d_0.01, 6 ^a , d_0.01
30	32747131	9	1 ^a , b, c, d, e_0.1, 1 ^a , b, c, d, e_0.01, 2 ^a , b, c, d, e_0.1, 2 ^a , b, c, d, e_0.01, 3 ^a , b, c, d, e_0.1, 3 ^a , b, c, d, e_0.01, 4 ^a , b, c, d, e_0.1, 4 ^a , b, c, d, e_0.01, 5 ^a , b, c, d, e_0.1, 5 ^a , b, c, d, e_0.01, 6 ^a , b, c, d, e_0.1, 6 ^a , b, c, d, e_0.01
31	32749768	9	3 ^d _0.1, 4 ^d _0.1
32	32749770	9	3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 6 ^d _0.1

(续表 2)

编号 Number	SNP 位点 SNP locus	染色体 Chr.	不同模型、显著水平下与 SNP 相关联的性状 Traits correlated with SNP under different analytical models and significant level
33	32752786	9	1 ^d _0.1, 2 ^d _0.1, 3 ^{b, d} _0.1, 3 ^d _0.01, 4 ^{b, d} _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
34	32753035	9	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
35	32973114	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
36	33118463	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
37	33145926	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{b, c, d} _0.1, 3 ^{c, d} _0.01, 4 ^{b, c, d} _0.1, 4 ^{c, d} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{b, c, d} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{b, c, d} _0.01
38	33145927	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
39	33148740	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
40	33156262	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
41	33170290	9	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
42	33170293	9	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
43	33211574	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
44	33222811	9	1 ^{c, d} _0.1, 1 ^d _0.01, 2 ^{c, d} _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^{c, d} _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
45	33229209	9	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1
46	33230719	9	3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
47	33243331	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
48	33244698	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
49	33283731	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
50	33283949	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
51	33288990	9	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
52	33302511	9	1 ^{b, c, d} _0.1, 1 ^d _0.01, 2 ^{b, c, d} _0.1, 2 ^d _0.01, 3 ^{b, c, d} _0.1, 3 ^d _0.01, 4 ^{b, c, d} _0.1, 4 ^d _0.01, 5 ^{b, c, d} _0.1, 5 ^d _0.01, 6 ^{b, c, d} _0.1, 6 ^d _0.01
53	33451096	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
54	33451119	9	1 ^{b, c, d} _0.1, 1 ^d _0.01, 2 ^{b, c, d} _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^{b, c, d} _0.1, 5 ^d _0.01, 6 ^{b, c, d} _0.1, 6 ^d _0.01
55	33480937	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
56	34878453	9	3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 6 ^d _0.1, 6 ^d _0.01
57	34898663	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{b, c, d} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{b, c, d} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
58	34898695	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{b, c, d, e} _0.1, 3 ^{b, c, d} _0.01, 4 ^{b, c, d, e} _0.1, 4 ^{b, c, d} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
59	34908783	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^d _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^d _0.01
60	34922341	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
61	34935499	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, c, d} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, c, d} _0.01, 3 ^{a, d} _0.1, 3 ^d _0.01, 4 ^{a, d} _0.1, 4 ^d _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, c, d} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, d} _0.01
62	34959324	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01

(续表 2)

编号 Number	SNP 位点 SNP locus	染色体 Chr.	不同模型、显著水平下与 SNP 相关联的性状 Traits correlated with SNP under different analytical models and significant level
63	34964634	9	1 ^d _0.1, 2 ^d _0.1
64	34998000	9	1 ^d _0.1, 2 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
65	35003777	9	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
66	35060347	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
67	35065836	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
68	35097925	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
69	35097926	9	3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
70	35114336	9	3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 4 ^d _0.01, 5 ^d _0.1, 6 ^d _0.1
71	35117629	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, c, d, e} _0.01, 3 ^{a, d, e} _0.1, 3 ^d _0.01, 4 ^{a, b, d, e} _0.1, 4 ^d _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, d} _0.01
72	35123523	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
73	35123542	9	1 ^{a, b, c, d, e} _0.1, 1 ^{b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{b, c, d} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{b, c, d} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
74	35123599	9	3 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
75	35180852	9	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 6 ^d _0.1
76	35212385	9	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^{b, c, d} _0.1, 3 ^{b, c, d} _0.01, 4 ^{b, c, d} _0.1, 4 ^{b, d} _0.01, 5 ^{b, c, d} _0.1, 5 ^d _0.01, 6 ^{b, c, d} _0.1, 6 ^d _0.01
77	35212534	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
78	35253233	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, d, e} _0.1, 3 ^d _0.01, 4 ^{a, d, e} _0.1, 4 ^{d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, d, e} _0.01
79	35254558	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{b, c, d} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{b, c, d} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{b, c, d} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{b, c, d} _0.01
80	35256410	9	1 ^{a, b, c, d, e} _0.1, 1 ^{a, b, c, d, e} _0.01, 2 ^{a, b, c, d, e} _0.1, 2 ^{a, b, c, d, e} _0.01, 3 ^{a, b, c, d, e} _0.1, 3 ^{a, b, c, d, e} _0.01, 4 ^{a, b, c, d, e} _0.1, 4 ^{a, b, c, d, e} _0.01, 5 ^{a, b, c, d, e} _0.1, 5 ^{a, b, c, d, e} _0.01, 6 ^{a, b, c, d, e} _0.1, 6 ^{a, b, c, d, e} _0.01
81	8842711	11	1 ^d _0.1, 2 ^d _0.1, 3 ^d _0.1, 3 ^d _0.01, 4 ^d _0.1, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01
82	23995788	12	1 ^d _0.1, 1 ^d _0.01, 2 ^d _0.1, 2 ^d _0.01, 3 ^d _0.1, 4 ^d _0.1, 5 ^d _0.1, 5 ^d _0.01, 6 ^d _0.1, 6 ^d _0.01

1: AUDPC_2015; 2: sAUDPC_2015; 3: AUDPC_2016; 4: sAUDPC_2016; 5: AUDPC_mean; 6: sAUDPC_mean; a: CMLM 模型; b: EMMAX 模型; c: FASTLMM 模型; d: GLM 模型; e: MLM 模型; 显著水平分别为 0.1 和 0.01。

1: AUDPC_2015; 2: sAUDPC_2015; 3: AUDPC_2016; 4: sAUDPC_2016; 5: AUDPC_mean; 6: sAUDPC_mean; a: CMLM; b: EMMAX; c: FASTLMM; d: GLM; e: MLM; significant difference at the 0.1 and 0.01 probability levels.

同源基因(*R8*)和 *Rpi-vnt1* 以及编码多效性耐药蛋白基因; 5 个基因编码 MAPK 蛋白和 WRKY 转录因子; 1 个基因参与茉莉酸途径; 3 个基因与水杨酸途径相关; 6 个基因是病程相关的基因; 3 个基因参与苯基丙酸类合成途径; 其他与晚疫病抗性相关的基因如 HMGR 基因(2 个)、细胞色素 P450 (21 个)。

3 讨论

3.1 不同模型分析对全基因关联分析结果的影响

本研究采用了 5 种模型对基因组数据和表型数据进行关联分析。GLM 模型(general linear model)

采用 Q 矩阵^[16], MLM 模型(mixed linear model)采用 Q+K 矩阵^[16], CMLM 模型(compressed mixed linear model)算法介于 GLM 和 MLM 之间, 寻找最优算法压缩计算时间^[20], EMMAX 模型(efficient mixed model association eXpedited)在 MLM 模型基础上校正关联群体的群体结构和遗传亲缘关系并加速这种运算过程^[21-22], FASTLMM (factored spectrally transformed linear mixed model)同样修正了 MLM 模型的运算公式, 提高运算速度^[23]。尽管不同的模型存在差异, 但是在所有模型下分析的表型性状得到的结果都比较可靠(图 2)。5 种模型下共关联到 82 个 SNP 位点, 而同一性状、同样的显著水平下, GLM

图 3 GWAS 分析生成的曼哈顿图

Fig. 3 Manhattan plots of GWAS

A: GLM 模型分析 AUDPC_mean 性状; B: GLM 模型分析 AUDPC_16 性状; C: EMMAX 模型分析 sAUDPC_16 性状; D: GLM 模型分析 AUDPC_15 性状。

A: AUDPC_mean using GLM model; B: AUDPC_16 using GLM model; C: sAUDPC_16 using EMMAX; D: AUDPC_15 using GLM model.

模型分析关联到的 SNP 位点数量明显多于其他模型 (表 2)。与晚疫病抗性相关的候选基因中, 关联到 48 个 SNP 位点, 其中 13 个 (第 6、14、16、31、32、56、60、65、68、69、70、75 和 81 号) SNP 位点只在 GLM 模型下关联到, 16 个 SNP 位点在所有模型到关联到, 剩余的 19 个 SNP 位点在 2~4 个模型下获得。因此, 利用多种模型分析能关联到更多可能与晚疫病抗性相关的候选基因。

3.2 马铃薯晚疫病水平抗性群体中可能存在的抗性基因

栽培马铃薯晚疫病抗性主要来自安第斯栽培种 *S. tuberosum* Andigenum group (包括 *andigena*、*phureja* 和 *stenotomun*)^[24-26], 并通过导入野生种如 *S. demissum*^[27]、*S. venturii*^[7]、*S. bulbocastanum*^[28] 等的抗性基因不断改良马铃薯栽培种的晚疫病抗性。尽管国际马铃薯中心通过不断的轮回选择创制了一批晚疫病水平抗性群体^[29], 但是这批材料中可能仍存在垂直抗性基因 (*R1-R11*)^[30]。本研究所用的试验材料即是来自国际马铃薯中心筛选的水平抗性群体, 并且关联到 12 个 *R1* 类似基因, 3 个番茄斑萎病抗性基因, 4 个 *Rpi-vnt1* 抗性基因以及 4 个多效性耐药蛋白基因。

植物中抗性基因编码的最大的一类蛋白具有核

苷酸结合位点和亮氨酸重复结构 (nucleotide-binding site plus leucine-rich repeat, NB-LRR)^[31], 而目前已知的马铃薯晚疫病抗性基因编码的都是 NB-LRR 蛋白^[32]。*R1* 基因定位在 5 号染色体上, 是植物抗性基因亮氨酸 zipper/NBS/LRR 中的一员^[33]。根据前人的研究, 至少有 4 个抗性基因位于 9 号染色体, 分别是 *R8*^[8-9]、*R9a*^[34]、*Rpi-vnt1*^[7] 和 *Rpi-moc1*^[35], 这 4 个基因均位于 9 号染色体长臂末端, 而且遗传距离比较近^[34,36]。本研究所关联到的 12 个 *R1* 类似基因位于 9 号染色体, 其长度为 35.34 Mb, 而关联到的 SNP 的位置在 34.8 Mb 左右, 因此, 这些抗性基因肯定不是 *R1*, 而可能是已克隆的 *R8* 或其他抗性基因。*Sw-5* 是番茄中一类广谱抗性的番茄斑萎病 (ToMV) 抗性基因^[37], 位于 9 号染色体上的抗性基因 *R8* 与 *Sw-5* 同源, 而 *Rpi-vnt1* 与番茄中另 1 个 ToMV 持久抗性基因 Tm-2² 同源^[7,38]。本研究中另外关联到与 *Rpi-vnt1* 基因类似的基因, 其位置在 32.5 Mb 附近, 而关联到的 ToMV 抗性基因位于 34.7 Mb 左右, 根据 *R8* 与 *Rpi-vnt1* 的遗传位置^[36], *Rpi-vnt1* 在 *R8* 的上方, 因此关联到位于 32.5 Mb 的基因可能是 *Rpi-vnt1*, 而位于 34.7 Mb 的基因可能是 *R8*。多效性耐药蛋白是一类 ABC 转运蛋白, 可参与到拟南芥^[39] (*PEN3*) 和小麦^[40] (*Lr34*) 中非宿主抗性和对病原菌的持久抗

表 3 根据基因参与途径或分类筛选的晚疫病抗性候选基因

Table 3 Candidate genes for late blight resistance, grouped by pathway or category						
基因分类	基因编号	染色体	起点	终点	SNP 位置	基因注释
Gene category	Gene ID	Chr.	Start position	End position	SNP position	Gene annotation
抗性基因 Resistance gene	g25436.tl	9	34805916	34807385	34898663; 34898695	预测: 晚疫病抗性蛋白 R1A-3 同源物
	g25437.tl	9	34807412	34808052	34898663; 34898695	Predicted: late blight resistance protein homolog R1A-3
	g25431.tl	9	34780278	34784653	34878453	
	g25432.tl	9	34786541	34790317	34878453	
	g25432.i2	9	34786541	34790036	34878453	
	g14640.tl	9	31687872	31696553	31707832; 32973114	预测: 多效性耐药蛋白 1 类似物
	g14640.tl.1.57a38f03	9	31688945	31696553	31707832; 32973114	Predicted: pleiotropic drug resistance protein 1-like
	g14641.tl	9	31703080	31710355	31707832; 32973114	
	g14641.i2	9	31705373	31710210	31707832; 32973114	
	g23609.i2	9	33401684	33406094	33451096; 33480937	预测: 晚疫病抗性蛋白 R1-A 类似物
	g25422.tl	9	34689253	34694184	35212534; 35253233; 35254558; 35256410	Predicted: late blight resistance protein R1-A-like
	g25423.tl	9	34705548	34707452	35253233; 35254558; 35256410	预测: 番茄斑萎病毒抗性蛋白; Sw-5
	g25424.tl	9	34707468	34709397	35253233; 35254558; 35256410	Predicted: tospovirus resistance protein; Sw-5
	g25435.tl	9	34803602	34805449	34898663; 34898695	预测: 晚疫病抗性蛋白 R1B-17 同源物
	g23609.tl	9	33403372	33406094	33451096; 33480937	Predicted: late blight resistance protein homolog R1B-17
	g25441.tl	9	34858961	34861507	34898663; 34898695; 34935499	预测: 晚疫病抗性蛋白 R1B-16 同源物
	novel_model_287_57a387f8	9	34793994	34794640	34878453	Predicted: late blight resistance protein homolog R1B-16
	g25442.tl	9	34868973	34870358	34898663; 34898695; 34935499; 34959324	预测: 晚疫病抗性蛋白 R1B-12 同源物
g25443.tl	g25443.tl	9	34870487	34871985	34898663; 34898695; 34935499; 34959324	Predicted: late blight resistance protein homolog R1B-12
		9	32596314	32599362	32627854; 32642867; 32973114	预测: 晚疫病抗性蛋白 R1B-13 同源物
		9	32586857	32588029	32627854; 32642867; 32973114	Predicted: late blight resistance protein homolog R1B-13
		9	32588125	32589258	32627854; 32642867; 32973114	Predicted: Rpi-vnt1 类似蛋白
		9	32742488	32745094	32627854; 32642867; 32973114	Predicted: Rpi-vnt1-like protein
		9	33145927; 33148740; 33156262; 33211574; 33244698			预测: Rpi-vnt1; 病害抗性蛋白 RPP13 类似物
g30364.tl	g30364.tl	9				Predicted: Rpi-vnt1, disease resistance RPP13-like protein
		9				3-like
g30365.tl	g30365.tl	9				
		9				
g30379.tl	g30379.tl	9				
		9				

(续表 3)

基因分类	基因编号	染色体	起点	终点	SNP 位置	基因注释
Gene category	Gene ID	Chr.	Start position	End position	SNP position	Gene annotation
信号转导和基因调控						
	g9062.t2	7	35625094	35630598	37485429	预测: 丝裂原活化蛋白激酶 20 类似物
Signal transduction and gene regulation						
	g9069.t1	7	35704028	35707186	37485429	Predicted: mitogen-activated protein kinase 20-like isoform X2
	g9374.t1	3	32070422	32071072	32015964	预测: WRKY 转录因子 71 类似物
	g9375.t1	3	32072369	32072977	32015964	Predicted: WRKY transcription factor 71-like
	g9378.t1	3	32077976	32078758	32015964	预测: WRKY 转录因子 50
						Predicted: probable WRKY transcription factor 50
						预测: WRKY 转录因子 22 类似物
						Predicted: WRKY transcription factor 22-like
茉莉酸途径						
Jasmonate acid pathway						
	g25456.t1	9	34996977	34998050	34898663; 34898695; 34908783; 34922341; 34935499; 34959324; 35003777; 35060347; 35065836	预测: 紫松果黄素类似蛋白
水杨酸途径						
Salicylic acid pathway						
	g14626.t1	9	31580629	31582530	32973114	预测: S-腺苷-L-蛋氨酸: 水杨酸羧甲基转移酶
	g14626.t1.1.57a38f03	9	31580631	31582517	32973114	Predicted: S-adenosyl-L-methionine: salicylic acid carboxyl methyltransferase
	g14626.t1.2.57a38f03	9	31580629	31582530	32973114	
病程相关基因						
Pathogenesis-related genes						
	g14872.t1	11	7666287	7670146	8842711	预测: 病程相关蛋白 5
	g19297.t1	9	30419374	30420192	30491004; 30518418	Predicted: pathogenesis-related protein 5
	g19298.t1	9	30423198	30424344	30491004; 30518418; 30522602	预测: 病程相关蛋白 STH-2
	g19299.t1	9	30428591	30429746	30491004; 30518418; 30522602	Predicted: pathogenesis-related protein STH-2
	g19300.t1	9	30432772	30434275	30491004; 30518418; 30522602	预测: 病程相关蛋白 STH-2 类似物
	g19301.t1	9	30437383	30438544	30491004; 30518418; 30522602	Predicted: pathogenesis-related protein STH-2-like
苯基丙酸类合成途径						
Phenylpropanoid pathway						
	g14619.t1	9	31524451	31526599	32747131; 32749768; 32749770; 32752786; 32753035	马铃薯查尔酮合成酶 1A
	g14620.t1	9	31529489	31531247	32747131; 32749768; 32749770; 32752786; 32753035	<i>Solanum tuberosum</i> chalcone synthase 1a (CHS1A)
	g14621.t1	9	31531305	31535134	32747131; 32749768; 32749770; 32752786; 32753035	马铃薯查尔酮合成酶 1B
						<i>Solanum tuberosum</i> chalcone synthase 1b
其他 Others						
HMGR gene						
	g28243.t1	11	8756852	8757364	8842711	预测: 3-羟基-3-甲基戊二酰辅酶 A 还原酶 1 类似物
	g28244.t1	11	8757438	8762746	8842711	Predicted: 3-hydroxy-3-methylglutaryl-coenzyme A reductase 1-like

(续表 3)

基因分类	基因编号	染色体	起点	终点	SNP 位置	基因注释
Gene category	Gene ID	Chr.	Start position	End position	SNP position	Gene annotation
细胞色素 P450 Cytochrome P450	g21325.t1	9	34334505	34336163	35060347; 35065836; 35097925; 35097926; 35097926;	预测: 细胞色素 P450 94A1 类似物
					35114336; 35117629; 35123523; 35123542; Predicted: cytochrome P450 94A1-like	
					35180852; 35212385; 35212534	
	g21326.t1	9	34343448	34344762	35060347; 35065836; 35097925; 35097926;	
					35114336; 35117629; 35123523; 35123542;	
					35180852; 35212385; 35212534	
	g23607.t1	9	33393062	33396075	33302511; 33451096; 33451119; 33480937	预测: 细胞色素 P450 83B1 同型类似物
					33302511; 33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23608.t1	9	33398392	33399778	33451096; 33451119; 33480937	预测: 细胞色素 P450 83B1 类似物
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23610.t1	9	33406593	33411641	33451096; 33451119; 33480937	Predicted: cytochrome P450 83B1-like isoform X1
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23611.t1	9	33416184	33418529	33451096; 33451119; 33480937	预测: 细胞色素 P450 83B1 类似物
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23612.t1	9	33424076	33426004	33451096; 33451119; 33480937	Predicted: cytochrome P450 83B1-like
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23613.t1	9	33429788	33431643	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23614.t1	9	33432366	33434050	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23615.t1	9	33437050	33437607	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23617.t1	9	33453168	33454903	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23618.t1	9	33463599	33463985	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23619.t1	9	33464022	33465496	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23620.t1	9	33466928	33470627	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23621.t1	9	33474712	33478148	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23622.t1	9	33479828	33481648	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23623.t1	9	33488499	33490300	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23624.t1	9	33493893	33496239	33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23625.t1	9	33498096	33499868	33451096; 33451119; 33480937	预测: 细胞色素 P450 71A1 类似物
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g23616.t1	9	33451091	33452431	33451096; 33451119; 33480937	Predicted: cytochrome P450 71A1-like
					33451096; 33451119; 33480937	
					33451096; 33451119; 33480937	
	g18525.t1	3	30978254	30981292	32015964	预测: 细胞色素 P450 71A1 类似物
					32015964	
					32015964	

性中。马铃薯中的多效性耐药蛋白也可参与到晚疫病病菌的侵染过程中,但是具体怎么调节这个过程尚不清楚^[41]。本研究关联到的多效性耐药蛋白基因位于 31.7 Mb 左右,其对马铃薯晚疫病抗性贡献的大小,有待进一步研究。

3.3 其他可能影响马铃薯晚疫病抗性的相关基因

本研究所用材料主要是表现出晚疫病水平抗性,即非 *R* 基因主导的持久抗性^[29]。还存在其他途径影响晚疫病抗性^[42-43],包括参与信号转导和基因调控、茉莉酸途径、水杨酸途径、病程相关基因、苯基丙酸类合成途径、HMGR 基因和细胞色素 P450。马铃薯中 MAPK 激酶和 WRKY 转录因子可参与植物对晚疫病病菌的防御过程如 *StMPK1*^[44]、*StWRKY8*^[45]、*StWRKY1*^[46]。本研究在 7 号染色体上关联到 1 个 MAPK 基因和 WRKY 基因,在 3 号染色体上关联到 3 个 WRKY 基因,它们对晚疫病水平抗性的贡献有待进一步研究。激素信号在植物病害防御中发挥着重要作用,植物激素茉莉酸和水杨酸代谢途径中的因子不同程度地参与到马铃薯晚疫病水平抗性中^[47-49]。本研究中关联到 1 个与茉莉酸代谢途径可能相关和 3 个与水杨酸代谢途径可能相关的基因,在其他马铃薯晚疫病抗性全基因组关联分析和 QTL 定位研究中也定位到与茉莉酸和水杨酸代谢途径相关的基因^[50-51]。有趣的是,本研究中关联到 3 个参与苯基丙酸类合成途径的查尔酮合成酶基因(*CHS*),位于 9 号染色体。马铃薯中 *CHS* 基因至少有 6 个拷贝,研究较多的是位于 5 号染色体的 *CHS* 基因参与马铃薯块茎中花青素合成^[52-54]。但是,查尔酮合成酶能够参与植物病害防御反应^[55-56],表明位于 9 号染色体的 *CHS* 基因可能是构成马铃薯晚疫病水平抗性因素之一。其他基因包括与病程相关的基因、HMGR 基因和细胞色素 P450 都有报道可以参与植物病害防御过程,但是在马铃薯晚疫病水平抗性中所起的作用是不清楚的,而本研究关联到的基因可以为马铃薯晚疫病水平抗性的形成机理提供参考^[42,57-59]。

4 结论

基于 5 种模型的 GWAS 结果,共检测到 82 个与晚疫病抗性显著相关的 SNP 位点,其中 48 个位点关联到可能与晚疫病抗性相关的候选基因,包括 *R1* 同源基因、*Sw-5* 同源基因(*R8*)、*Rpi-vnt1* 基因、与信号转导相关的 MAPK 基因、WRKY 基因、参与植物激素茉莉酸和水杨酸代谢相关的基因、参与苯基丙

酸类合成途径的查尔酮酶基因和其他病程相关的基因、HMGR 基因以及细胞色素 P450 基因。

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