苹果黑星病研究进展

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摘要 苹果黑星病是苹果重要的病害之一，发病严重时可导致苹果严重减产和品质下降。该病害在世界上许多国家都有发生，各国对苹果黑星病的分布、流行规律、病原菌致病性、生物学特性、寄主的抗病性及抗病基因、防治方法和病害监测等方面进行了广泛深入的研究。本文综合近年来的文献资料，从苹果黑星病病原菌、致病机制和抗病机理、防控技术、抗药性、检测方法及预测预报等方面进行了阐述，以期为该病害的绿色防控提供科学依据。

关键词 苹果黑星病；病原菌；致病机制；抗病机理；防控技术；抗药性；检测方法；预测预报

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Research Progress of Apple Scab

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Abstract Apple scab is one of the most important diseases of apples. When the disease is serious, it can lead to severe reduction of apple yield and quality. The disease has occurred in many countries around the world. Many countries have conducted extensive and in-depth research on the distribution, epidemic law, pathogenicity, biological characteristics, host disease resistance and disease resistance genes, control methods and disease monitoring of apple scab. Based on the literature in recent years, this paper expounded the pathogen, pathogenic mechanism and disease resistance mechanism, prevention and control technology, drug resistance, detection methods and prediction of apple scab, so as to provide a scientific basis for the green prevention and control of the disease.

Keywords apple scab; pathogen; pathogenic mechanism; disease resistance mechanism; prevention and control technology; drug resistance; detection method; prediction

苹果黑星病在世界上许多国家都有发生，该病可导致苹果果实品质变劣和产量下降，发病严重时可减产40%左右，是阻碍苹果产业发展的重要病害之一。苹果黑星病是由真菌 *Venturia inaequalis* 引起的，可侵染叶片、果实、叶柄、花、萼片、花梗、细枝和芽鳞等，主要危害叶片和果实，严重时常造成落叶、落果和果实开裂畸形。表现症状有泡斑型、边缘坏死型、干枯型、褪绿型、梭斑型、疮痂型，其典型症状为泡斑型。苹果黑星病的症状表现与病原菌和寄主之间关系密切，当病原菌和寄主非亲和时，不表现症状；当病原菌和寄主亲和时，表现症状并能产生大量的分生孢子；病原菌与含有抗性基因的寄主互作时，则症状轻，产孢少[1]。

1 苹果黑星病病原菌

瑞典植物学家Elias Fries最先描述了苹果黑星菌的无性阶段，Cooke发现了病原菌的有性阶段，Goethe结合有性阶段和无性阶段最终确定该病原菌为苹果黑星菌。据报道，不同地区分离的黑星菌菌株生物学特性存在显著差异，主要表现在分生孢子的大小、菌落颜色及边缘平滑程度、菌丝生长速度、产孢强度等方面。

苹果黑星菌在很多地区以子囊孢子越冬。冬季

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气候寒冷有利于假囊壳形成,子囊孢子在冬季落叶上的假囊壳中产生,为最重要的初侵染源,在病害发生和流行过程中起到十分重要的作用。降水、叶片湿度和较高的相对湿度可以加速子囊孢子的成熟,降雨是促进子囊孢子发育的第一因素[2-3]。子囊孢子的释放与降雨和光照关系密切,也受结露的影响。在苹果树开花期间,干燥天气大于 7 d 的年份中,子囊孢子的释放时间明显延迟[4]。成熟的子囊孢子从苹果树萌芽开始,遇到下雨立即释放,并保持 24 h 无间断持续释放;在连续降雨的情况下,前 2 d 子囊孢子释放量最大,释放时间可持续 3~4 d。晚上 23:00 至第 2 天凌晨 4:00 子囊孢子释放率不超过 1%;在日出 3 h 之后,温度 0~5 ℃时孢子释放率 0.8%,5~10 ℃时孢子释放率 3%,10 ℃以上时孢子释放率 8.1%;日出 8~11 h 后,子囊孢子释放率均超过 50%[5]。子囊孢子在树冠内不是随机分布的,树冠中心的子囊孢子密度最高,在树冠的中心和西部边缘子囊孢子沉积最多[6]。

在少数地区,分生孢子也能越冬。在荷兰的有机果园和混栽果园中,分生孢子越冬广泛存在[7]。在英格兰东北部的果园中,分生孢子在病害循环初侵染源中占病原菌的 20%~50%[8]。

不同品种苹果黑星菌的分离株基因型差异显著,同一果园中相同品种分离株基因型也有显著差异,不同栽培品种的苹果黑星菌种群差异显著,在混栽果园中随着时间的推移仍存在苹果黑星菌种群的分化[9-10]。有研究表明,对土耳其 2 个不同区域的苹果黑星菌基因进行多样性调查,经 PCR 分析确定分别属于 5 个不同的族群。苹果黑星病在不同品种果树上的潜育期不同,病原菌在不同品种果树叶片上的产孢量也存在显著差异[11]。在病菌侵染过程中,最幼嫩的叶片所需时间最短,约为 5 h,约 50%的病斑在侵染 7 h 后出现;具有抗性的叶片则需要更长的时间[5]。

2 苹果黑星菌致病机制和苹果树抗病机理

苹果黑星菌孢子在接种叶片后 12 d 可形成分支,随后扩展至角质层,通过反复辐射分支,在叶片表面形成网络[12]。黑星菌能侵染感病品种所有龄期的叶片,在叶片角质层下形成大量病斑,在不同龄期的叶片上,病斑大小和菌丝形态差异很大,在发育成熟的抗病叶片上,菌丝扩展受到了来自寄主组织结构方面的阻碍[13]。

苹果树对苹果黑星菌存在天然的抗性。Zajícová 等[14]使用扫描电子显微镜、透射显微镜和荧光显微镜比较苹果幼叶和老叶表皮不同个体发育阶段的近轴表面,分析叶片角质层结构、细胞壁组成发育以及表皮细胞扩张与抗病性之间的关系,发现细胞壁中的多糖可能对菌丝体生长起一定作用。Pagès 等[15]报道,臭氧可以改变细胞膜,氧化膜磷脂,导致细胞表面脆化和流动性改变,从而抑制分生孢子的发育。在病原菌攻击时,水杨酸可以触发多种植物防御反应。Sarkate 等[16]用苹果黑星菌诱导子处理苹果细胞培养物发现,经过诱导,水杨酸积累水平增加了 5.6 倍。Usenik 等[17]分析了苹果叶片中黄酮醇与苹果抗黑星病的关系,发现在抗性品种中酚 173 的相对含量更高。Hutabarat 等[18]研究表明,转基因苹果植株中查尔酮 3-羟化酶基因过度表达引起 3-羟色胺的积累增加,可降低苹果黑星病感病能力。Gołebiowski 等[19]认为,苹果皮中儿茶素和表儿茶素含量高的苹果对黑星病更有抵抗力。Mansoor 等[20]研究发现,多酚的合成和积累与对苹果黑星病的抗病性密切相关,苹果中含有丰富的酚类化合物,可增强对苹果黑星菌的抵抗力。梁振宇[21]测定了感染苹果黑星病的叶片内 POD、SOD、PPO 和 PAL 等 4 种酶活性变化,并确定这 4 种酶均不同程度地参与了寄主对病原物入侵的防御。Sikorskaite-Gudziuniene 等[22]从分子机制方面证明,泛素/26S 蛋白酶体介导的蛋白质降解、蛋白质折叠、碳水化合物代谢有利于苹果抵抗黑星病侵染。Cova 等[23]则阐述了水杨酸可能不参与苹果黑星病防御机制。

苹果黑星菌在抗病品种叶片中的扩展会受到寄主组织的限制,虽然仍能大量发生,但在叶片外观上并不表现症状。胡小平等[24]通过透射电镜观察,新疆野苹果叶片的角质层厚度显著高于富士和嘎啦,新疆野苹果的病害严重度最低,抗病性主要表现在抗侵入和抗扩展两个方面。

3 苹果黑星病的防控技术

苹果黑星病的防治主要依赖化学药剂，国内外学者对防治苹果黑星病的杀菌剂的最佳施用时间、施用浓度及防治效果、农药残留等方面进行了诸多报道。在初花期至盛花期，叶片喷施琥珀酸脱氢酶抑制剂、铜基及代森类杀菌剂、脱甲基化抑制剂(DMI)杀菌剂、甲氧基丙烯酸酯类(QoI)杀菌剂等能有效防止病害的发生及扩展[25-30]。

在有机苹果生产中，农业防治起着举足轻重的作用。通过秋季收集落叶并粉碎、冬末果园地面覆盖稻草或塑料箔发现，苹果黑星菌子囊孢子的产生、黑星病发病率和严重度都有下降[31-32]。Didelota 等[33]发现，种植抗病品种结合保持田园卫生不仅可降低杀菌剂的使用，还能提高对病害的可持续控制。Ekinci 等[34]用感染苹果黑星病的叶片和牛粪制作堆肥，通过发酵即可有效杀灭病原菌，减轻病害发生程度，也可以可靠地用于农业生产。

培育抗病品种是解决苹果黑星病危害长期有效的途径，许多国家正在利用分子生物学手段寻找抗病新基因，并设法通过育种手段把抗病基因引入新品种中。在现有的苹果品种中，已经鉴定出 20 多个主要的抗苹果黑星病基因，并且对多个基因进行了定位，开发了相应的分子标记，对少数基因进行了克隆和功能研究[35-42]。其中，*Rvi6* 基因在不同的育种项目中应用最为广泛，*Rvi2*、*Rvi4*、*Rvi5*、*Rvi10*、*Rvi11*、*Rvi12*、*Rvi13* 和 *Rvi15* 等 8 个基因在育种过程中也有所应用。

苹果植株对苹果黑星菌的抗性可以遗传，野苹果作为抗病种质资源在世界各地已引起高度重视，野外苹果黑星病易感性多样是苹果育种的抗性来源。Paris 等[43]用从野生苹果(*Malus floribunda* 821)中获得的 *HcrVf2* 基因改造感病品种嘎啦及其变种，可以使苹果对苹果黑星病产生抗病性。Karapetsi 等[44]对希腊国产苹果品种的抗黑星病基因进行了分子筛选，评估了 20 个本地区域中存在的 5 个抗性基因。Patocchi 等[45]在 2009—2018 年从 14 个国家收集了 9 000 个数据，发现 *Rvi5*、*Rvi11*、*Rvi12*、*Rvi14*、*Rvi15* 基因具有持久抗性，*Rvi1*、*Rvi3*、*Rvi8* 基因抗性经常被克服，*Rvi2*、*Rvi4*、*Rvi6*、*Rvi7*、*Rvi9*、*Rvi13* 对育种仍非常有用。抗黑星病品种有 Priscilla、Nova Easygro、Prima、Warner's King、Akane、Remo、Co-op25、Liberty、Batul、Citrom alma、Kanadai renet 等[46-47]。中国苹果中，高度抗病品种有新疆野苹果和秦冠[24]，新疆巩留县莫合野果林中的新疆野苹果黑星病病情指数最低，抗病性较强[48]。

生物防治对苹果黑星病的控制也具有一定的效果。枝孢霉 H39 的孢子悬浮液能减少 40%~69%黑星菌分生孢子的产生[49]。植物提取物丝兰可减轻苹果黑星病症状，抑制病原孢子形成和孢子萌发[50]。在苹果落叶上喷洒 30%~60%酵母提取液可以加速落叶腐烂，抑制子囊孢子成熟和 99%子囊孢子的释放[51]。喷洒厚朴树皮提取物，浓度为 1 mg/mL 时，平均防效可达 93%[52]。丁香、桉树、薄荷和香草精油对黑星菌抑菌效果均高于硫酸铜[53]。无患子的水提取物(AE)和溶解在水中的无患子的氯仿-甲醇果皮提取物(CME)可以明显减少苹果幼苗叶片上的苹果黑星病症状，抑制苹果黑星菌孢子形成[54]。尿素与 Bond Max 或 OWB 的组合可以降低 5%假囊壳和子囊孢子产生，有效减少越冬病原物初侵染源[55]。果聚糖具有直接抑制苹果黑星菌菌丝生长的作用，喷洒于苹果幼苗叶面上能够抑制孢子形成，减少苹果黑星病的发生概率[56]。

4 苹果黑星菌抗药性研究

随着化学农药的持续应用，在有些地区苹果黑星菌已对某些杀菌剂产生抗药性。1987 年，有研究发现，抗苯菌灵的苹果黑星菌对氨基甲酸苯酯类杀菌剂的交互抗性成负相关性。2000 年，Zheng 等[57]研究发现，苹果黑星菌的突变体能够改变氧化酶、呼吸作用等，使黑星菌对嘧菌酯敏感变成抗药。2001 年，高立强研究发现，苹果黑星菌的抗药性同 DMI 类杀菌剂的施用次数成线性正相关，病原菌对腈菌唑和腈苯唑的敏感性显著相关，二者之间存在交互抗性，不同施药史病原菌群体之间的抗药性存在遗传多样性。2003 年和 2015 年，有学者确定了新南威尔士州、新英格兰、大西洋中部和中西部、纽约和新英格兰各州苹果黑星菌对 DMI 类杀菌剂腈菌唑的耐药

性[58-60]。2021 年,Cordero-Limon 等[61]报道,黑星菌对腈菌唑和戊唑醇之间存在交叉抗性;Gur 等[62]研究发现,苹果黑星菌对 QoI 类杀菌剂的抗药性在以色列普遍存在。

在苹果黑星病化学防治过程中,尽管黑星菌种群对苯醚甲环唑和腈菌唑具有实际抗性,但这 2 种药剂仍对苹果黑星病具有非常好的防治效果。因为 DMI 类杀菌剂之间存在交叉敏感性倾向,所以苹果种植者在生产过程中应谨慎使用腈菌唑和苯醚甲环唑。建立敏感性基线可为田间苹果黑星菌的抗药性监测及有效药剂的选择和风险评估提供科学依据,有效指导病害防治。近年,已经建立了黑星菌对吡噻菌胺、氟吡菌酰胺和苯并烯氟菌唑、腈菌唑、苯醚甲环唑的敏感性基线[59-60,63]。

5 苹果黑星病的检测方法

早期检测技术的开发可以快速诊断、预测病害的暴发。随着分子生物学的发展,分子检测技术作为一种更快、更客观、更灵敏的方法,在苹果黑星病的预防中起到重要作用。商 蓓等[64]建立了苹果黑星病菌的分子检测方法,在 1 d 内即可完成对该病原菌的分子检测,对苹果黑星病菌基因组 DNA 检测的灵敏度为 100 fp/μL。Daniëls 等[65]于 2012 年使用围绕 5.8S 的特定内部转录间隔区 2(ITS2)区域设计的引物开发了黑星菌特异性实时 PCR 检测 rRNA 基因,使用 SYBR ® Green I 技术,检测灵敏度达 100 fg。2018 年 Nouri 等[66]采用近红外高光谱图像监测早期苹果黑星病的发生发展。Franco ortega 等[67]2020 年使用环介导等温扩增(LAMP)方法,可以在 1 h 内识别苹果黑星病。

6 苹果黑星病的预测预报

植物病害预测预报对抓住有利防治时机,及时指导防治及减少经济损失具有重要意义。Lalic 等[68]根据短期天气预报和病害发生条件,使用机器学习和简易气象站预测以及基于 Mills 模型来预测苹果黑星病的发生发展。胡小平等[69-70]开发出了“苹果黑星病春季流行模拟系统(SSASS)”,陈婧[71]和周书涛[72]构建了渭北旱塬苹果黑星病流行程度预测模型和中期预测模型。

7 结语

综上所述,国外近年来开发了苹果黑星病的生物防治和农业防治方法,抗病基因和抗病品种研究也较为深入广泛,尤其是已将抗病基因用于苹果的抗病育种过程中;国内在苹果黑星菌的抗病基因鉴定、抗病育种、生物防治及病原菌的抗药性研究等方面都落后于国际水平,有待于进一步深入研究,应加大投入,为我国苹果黑星病的防治打下更为坚实的基础。

8 参考文献

[1] BÉNAOUF G,PARISI L.Characterization of *Venturia inaequalis* pathogenicity on leaf discs of apple trees[J].European Journal of Plant Pathology,1998,104(8):785-793.

[2] JANKOWSKI P,MASNY S.Comparison of mathematical models of maturation rate of the airborne *Venturia inaequalis* (Cooke) Wint.ascospores in central Poland[J].Journal of Plant Diseases and Protection,2019,126(4):269-279.

[3] JANKOWSKI P,MASNY S.Influence of moisture on maturation rate of the *Venturia inaequalis* (Cooke) Wint. ascospores in central Poland[J].Journal of Plant Diseases and Protection,2020,127(2):155-163.

[4] VILLALTA O N,WASHINGTON W S,KITA N,et al.The use of weather and ascospore data for forecasting apple and pear scab in Victoria,Australia[J].Australasian Plant Pathology,2002,31(3):205-215.

[5] STENSVAND A,EIKEMO H,SEEM R C,et al.Ascospore release by *Venturia inaequalis* during periods of extended daylight and low temperature at Nordic latitudes[J].European Journal of Plant Pathology,2009,125(1):173-178.

[6] CARISSE O,ROLLAND D,TALBOT B,et al.Heterogeneity of the aerial concentration and deposition of ascospores of *Venturia inaequalis* within a tree canopy during the rain[J].European Journal of Plant Pathology,2007,117(1):13-24.

[7] HOLB I J,HEIJNE B,JEGER M J.The widespread occurrence of overwintered conidial inoculum of *Venturia inaequalis* on shoots and buds in organic and integrated apple orchards across the Netherlands[J].European Journal of Plant Pathology,2005,111(2):157-168.

[8] PASSEY T A J,SHAW M W,XU X M.Differentiation in populations of the apple scab fungus *Venturia inaequalis* on cultivars in a mixed orchard remain over time[J].Plant Pathology,2016,65(7):1133-1141.

[9] XU X M,HARVEY N,ROBERTS A,et al.Population vari-

ation of apple scab (*Venturia inaequalis*) within mixed orchards in the UK [J].European Journal of Plant Pathology,2013,135(1):97–104.

[10] MANSOOR S,AHMED N,SHARMA V,et al.Elucidating genetic variability and population structure in *Venturia inaequalis* associated with apple scab diseaseusing SSR markers[J].PLoS One,2019,14(11):e0224300.

[11] 郭世保,胡小平,杨家荣,等.苹果黑星病潜育期及其病原菌产孢量研究[J].西北农业学报,2005,14(3):15–17.

[12] 黄丽丽,康振生,郭井泉,等.黑星病菌在苹果叶片上的发育过程研究(英文)[J].菌物系统,2003(3):494–497.

[13] 李保华,董向丽,徐向明.苹果黑星病菌在叶组织内的扩展形态[J].莱阳农学院学报,2005,22(1):1–4.

[14] ZAJÍCOVÁ I,TIHLAŘÍKOVÁ E,CIFROVÁ P,et al.Analysis of apple epidermis in respect to ontogenic resistance–against *Venturia inaequalis* [J].Biologia Plantarum,2019,63:662–670.

[15] PAGÈS M,KLEIBER D,VIOLLEAU F.Ozonation of three different fungal conidia associated with apple disease:importance of spore surface and membrane phospholipid oxidation[J].Food Science & Nutrition,2020,8(10):5292–5297.

[16] SARKATE A,SAINI S S,KUMAR P,et al.Salicylaldehyde synthase activity from *Venturia inaequalis* elicitor–treated cell culture of apple[J].Journal of Plant Physiology,2018,221:66–73.

[17] USENIK V,MIKULI–PETKOVŠEK M,SOLAR A,et al. Flavonols of leaves in relation to apple scab resistance[J]. Journal of Plant Diseases and Protection,2004,111(2):137–144.

[18] HUTABARAT O S,FLACHOWSKY H,REGOS I,et al. Transgenic apple plants overexpressing the chalcone 3–hydroxylase gene of *Cosmos sulphureus* show increased levels of 3–hydroxyphloridzin and reduced susceptibility to apple scab and fire blight[J].Planta,2016,243(5):1213–1224.

[19] GOŁEBIOWSKI M,MALINSKI E,SZANKIN M,et al. Determination of catechin and epicatechin in the peel of apple varieties resistant and non–resistant to apple scab[J]. Chemical Papers,2010,64(6):729–733.

[20] MANSOOR S,SHARMA V,MIR M A,et al.Quantification of polyphenolic compounds and relative gene expression studies of phenylpropanoid pathway in apple (*Malus domestica* Borkh) in response to *Venturia inaequalis* infection[J].Saudi Journal of Biological Sciences,2020,27(12):3397–3404.

[21] 梁振宇.陕西苹果黑星菌的生物学特性及寄主的抗病机制研究[D].杨凌:西北农林科技大学,2006.

[22] SIKORSKAITE–GUDZIUNIENE S,HAIMI P,GELVONAUSKIENE D,et al.Nuclear proteome analysis of apple cultivar ‘Antonovka’ accessions in response to apple scab (*Venturia inaequalis*)[J].European Journal of Plant Pathology,2017,148(4):771–784.

[23] COVA V,PARIS R,TOLLER C,et al.Apple genes involved in the response to *Venturia inaequalis* and salicylic acid treatment[J].Scientia Horticulturae,2017,226:157–172.

[24] 胡小平,张吉光,陈婧,等.新疆野苹果和秦冠的抗黑星病特性[J].植物病理学报,2010,40(6):609–614.

[25] 王华,陈祥,陈卫民,等.六种杀菌剂防治苹果黑星病田间药效试验[J].现代农药,2011,10(1):48–50.

[26] VILLANI S M,AYER K,COX K D.Molecular characterization of the sdhB gene and baseline sensitivity to penthiopyrad,fluopyram,and benzovindiflupyr in *Venturia inaequalis*[J].Plant Disease,2016,100(8):1709–1716.

[27] FELIPINI R B,BONETI J I,KATSURAYAMA Y,et al. Apple scab control and activation of plant defence responses using potassium phosphite and chitosan[J].European Journal of Plant Pathology,2016,145(4):929–939.

[28] AYER K M,VILLANI S M,CHOI M W,et al.Characterization of the VisdhC and VisdhD genes in *Venturia inaequalis*,and sensitivity to fluxapyroxad,pydiflumetofen,inpyrfluxam,and benzovindiflupyr[J].Plant Disease,2019,103(6):1092–1100.

[29] AYER K M,CHOI M W,SMART S T,et al.The effects of succinate dehydrogenase inhibitor fungicide dose and mixture on development of resistance in *Venturia inaequalis*[J]. Applied and Environmental Microbiology,2020,86(17):e01196–20.

[30] CHATZIDIMOPOULOS M,LIOLIOPOULOU F,SOTIROPOULOS T,et al.Efficient control of apple scab with targeted spray applications[J].Agronomy,2020,10(2):217.

[31] HOLB I J.Effect of six sanitation treatments on leaf litter density,ascospore production of *Venturia inaequalis* and scab incidence in integrated and organic apple orchards[J]. European Journal of Plant Pathology,2006,115(3):293–307.

[32] VON DIEST S G,MEITZ–HOPKINS J C,MACHARDY W E,et al.The effect of leaf shredding on apple scab in South

African orchards[J].Plant Disease,2016,100(10):2094-2098.

[33] DIDELOT F,CAFFIER V,ORAIN G,et al.Sustainable management of scab control through the integration of apple resistant cultivars in a low-fungicide input system[J].Agriculture,Ecosystems & Environment,2016,217:41-48.

[34] EKINCI K,ÖZGÖNEN ÖZKAYA H,MEMICI M,et al. Composting of apple scab (*Venturia inaequalis*) infected leaves with dairy manure[J].Erwerbs-Obstbau,2021,63(3):263-271.

[35] KHAJURIA Y P,KAUL S,WANI A A,et al.Genetics of resistance in apple against *Venturia inaequalis* (Wint.) Cke[J].Tree Genetics & Genomes,2018,14(2):1-20.

[36] BUS V G M,RIKKERINK E H A,VAN DE WEG W E,et al.The *Vh2* and *Vh4* scab resistance genes in two differential hosts derived from Russian apple R12740-7A map to the same linkage group of apple[J].Molecular Breeding,2005,15(1):103-116.

[37] GYGAX M,GIANFRANCESCHI L,LIEBHARD R,et al. Molecular markers linked to the apple scab resistance gene *Vbj* derived from *Malus baccata* jackii[J].Theoretical and Applied Genetics,2004,109(8):1702-1709.

[38] PATOCCHI A,BIGLER B,KOLLER B,et al.*Vr2*:a new apple scab resistance gene[J].Theoretical and Applied Genetics,2004,109(5):1087-1092.

[39] GALLI P,BROGGINI G A L,KELLERHALS M,et al.High-resolution genetic map of the *Rvi15* (*Vr2*) apple scab resistance locus[J].Molecular Breeding,2010,26(4):561-572.

[40] SCHOUTEN H J,BRINKHUIS J,BURGH A,et al.Cloning and functional characterization of the *Rvi15* (*Vr2*) gene for apple scab resistance[J].Tree Genetics & Genomes,2014,10(2):251-260.

[41] SORIANO J M,MADDURI M,SCHAART J G,et al.Fine mapping of the gene *Rvi18* (*V25*) for broad-spectrum resistance to apple scab,and development of a linked SSR marker suitable for marker-assisted breeding[J].Molecular Breeding,2014,34(4):2021-2032.

[42] COVA V,BANDARA N L,LIANG W,et al.Fine mapping of the *Rvi5* (*Vm*) apple scab resistance locus in the 'Murray' apple genotype[J].Molecular Breeding,2015,35(10):1-12.

[43] PARIS R,COVA V,PAGLIARANI G,et al.Expression profiling in *HcrVf2*-transformed apple plants in response to *Venturia inaequalis*[J].Tree Genetics & Genomes,2009,5(1):81-91.

[44] KARAPETSI L,NIANIOU-OBEIDAT I,ZAMBOUNIS A,et al.Molecular screening of domestic apple cultivars for scab resistance genes in Greece[J].Czech Journal of Genetics and Plant Breeding,2020,56(4):165-169.

[45] PATOCCHI A,WEHRLI A,DUBUIS P H,et al.Ten years of VINQUEST:first insight for breeding new apple cultivars with durable apple scab resistance[J].Plant Disease,2020,104(8):2074-2081.

[46] SANDSKÄR B,GUSTAFSSON M.Classification of apple scab resistance in two assortment orchards[J].Genetic Resources and Crop Evolution,2004,51(2):197-203.

[47] PAPP D,KIRÁLY I,TÓTH M.Suitability of old apple varieties in organic farming,based on their resistance against apple scab and powdery mildew[J].Organic Agriculture,2016,6(3):183-189.

[48] 刁永强,许正,闫鹏,等.新疆野苹果资源类型表型性状鉴定及优异资源的初步筛选[J].经济林研究,2019,37(1):17-24.

[49] KÖHL J J,MOLHOEK W W M L,GROENENBOOM-DE HAAS B B H,et al.Selection and orchard testing of antagonists suppressing conidial production by the apple scab pathogen *Venturia inaequalis*[J].European Journal of Plant Pathology,2009,123(4):401-414.

[50] BENGTSSON M,WULFF E,LYNGS JØRGENSEN H J,et al.Comparative studies on the effects of a yucca extract and acibenzolar-S-methyl (ASM) on inhibition of *Venturia inaequalis* in apple leaves[J].European Journal of Plant Pathology,2009,124(2):187-198.

[51] PORSCHE F M,PFEIFFER B,KOLLAR A.A new phytosanitary method to reduce the ascospore potential of *Venturia inaequalis*[J].Plant Disease,2017,101(3):414-420.

[52] THUERIG B,RAMSEYER J,HAMBURGER M,et al.Efficacy of a *Magnolia officinalis* bark extract against grapevine downy mildew and apple scab under controlled and field conditions[J].Crop Protection,2018,114:97-105.

[53] MUCHEMBLED J,DEWEER C,SAHMER K,et al.Antifungal activity of essential oils on two *Venturia inaequalis* strains with different sensitivities to tebuconazole[J].Environmental Science and Pollution Research International,2018,25(30):29921-29928.

[54] PORSCHE F M,MOLITOR D,BEYER M,et al.Antifungal activity of saponins from the fruit pericarp of *Sapindus mu-*

korossi against *Venturia inaequalis* and *Botrytis cinerea*[J]. Plant Disease,2018,102(5):991-1000.

[55] BECKERMAN J,ABBOTT C.Comparative studies on the effect of adjuvants with urea to reduce the overwintering inoculum of *Venturia inaequalis*[J].Plant Disease,2019,103(3):531-537.

[56] SVARA A,TARKOWSKIŁ P,VAN RENSBURG H C J,et al.Sweet immunity:the effect of exogenous fructans on the susceptibility of apple (*Malus*×domestica borkh.) to *Venturia inaequalis* [J].International Journal of Molecular Sciences,2020,21(16):5885.

[57] ZHENG D S,OLAYA G,KÖLLER W.Characterization of laboratory mutants of *Venturia inaequalis* resistant to the strobilurin-related fungicide kresoxim-methyl[J].Current Genetics,2000,38(3):148-155.

[58] HETHERINGTON S D,GUNNING D A.Myclobutanil resistance in an isolate of *Venturia inaequalis* from New South Wales[J].Australasian Plant Pathology,2003,32(1):121.

[59] VILLANI S M,BIGGS A R,COOLEY D R,et al.Prevalence of myclobutanil resistance and difenoconazole insensitivity in populations of *Venturia inaequalis*[J].Plant Disease,2015,99(11):1526-1536.

[60] FREDERICK Z A,VILLANI S M,COX K D.The effect of delayed-dormant chemical treatments on demethylation inhibitor (DMI) sensitivity in a DMI-resistant population of *Venturia inaequalis*[J].Plant Disease,2015,99(12):1751-1756.

[61] CORDERO-LIMON L,SHAW M W,PASSEY T A,et al. Cross-resistance between myclobutanil and tebuconazole and the genetic basis of tebuconazole resistance in *Venturia inaequalis*[J].Pest Management Science,2021,77(2):844-850.

[62] GUR L,LEVY K,FARBER A,et al.Delayed development of resistance to QoI fungicide in *Venturia inaequalis* in Israeli apple orchards and improved apple scab management using fungicide mixtures[J].Agronomy,2021,11(2):396.

[63] 高立强,李贤成,杨家荣.新疆苹果黑星病菌野生型菌株对腈菌唑的敏感性基线[J].菌物学报,2021,40(3):547-556.

[64] 商蓓,付洁,罗泽青,等.苹果黑星病菌的分子检测[J].西北农林科技大学学报(自然科学版),2010,38(8):104-110.

[65] DANIËLS B,DE LANDTSHEER A,DREESEN R,et al. Real-time PCR as a promising tool to monitor growth of *Venturia* spp. in scab-susceptible and-resistant apple leaves[J].European Journal of Plant Pathology,2012,134(4):821-833.

[66] NOURI M,GORRETTA N,VAYSSE P,et al.Near infrared hyperspectral dataset of healthy and infected apple tree leaves images for the early detection of apple scab disease[J]. Data in Brief,2018,16:967-971.

[67] FRANCO ORTEGA S,PRENCIPE S,GULLINO M L,et al.New molecular tool for a quick and easy detection of apple scab in the field[J].Agronomy,2020,10(4):581.

[68] LALIC B,FRANCIA M,EITZINGER J,et al.Effectiveness of short-term numerical weather prediction in predicting growing degree days and meteorological conditions for apple scab appearance[J].Meteorological Applications,2016,23(1):50-56.

[69] 胡小平,陈婧,周书涛,等.渭北旱塬苹果黑星病春季流行模拟系统[J].西北农业学报,2009,18(5):127-132.

[70] 胡小平,田雪亮,李随院,等.渭北旱塬苹果黑星病流行程度预测[J].西北农林科技大学学报(自然科学版),2007,35(10):151-154.

[71] 陈婧.苹果黑星病传播路线及长期预测模型[D].杨凌:西北农林科技大学,2009.

[72] 周书涛.渭北旱塬苹果黑星病中长期远程预测系统[D].杨凌:西北农林科技大学,2010.