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Field apple scab susceptibility of a diverse *Malus* germplasm collection identifies potential sources of resistance for apple breeding

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Abstract

Background: Breeding for resistance to apple scab (caused by *Venturia inaequalis*), the most devastating fungal disease of apples, relies on genetic resources maintained in germplasm collections.

Methods: To identify new sources of scab resistance, we evaluated 177 *Malus* accessions, including 27 primary and 13 hybrid *Malus* species from diverse geographical origins, in an orchard at Geneva, New York. We also screened a differential host set for 2 years to monitor for changes in the effectiveness of ten known scab resistance genes, which allowed us to confirm the presence of virulent pathogen races in the orchard.

Results: We found that ~ 37% of the wild *Malus* accessions and domesticated cultivars were resistant to apple scab in the field. Several of these accessions were unrelated to sources of previously known resistance genes and are promising for apple scab genetic research and resistance breeding. Cultivars carrying the *Rvi6* (*Vf*) gene from *Malus floribunda* clone 821, e.g. 'Liberty' or 'Florina', remained resistant despite the breakdown of *Rvi6*. 'Demir', a *Malus* hybrid from Turkey, and 'Chisel Jersey', a traditional English hard cider cultivar, showed fewer symptoms than the *Rvi6* resistant cultivar 'Prima'. Races 1 to 7 and 9 of *V. inaequalis* were present in the orchard, but no scab was observed on the indicator host accessions for races 11 and 12.

Conclusions: Detailed and systematic screening of *Malus* germplasm identified resistant and moderately resistant donor accessions based on resistance reaction types. These accessions are promising for use in future genetic studies to identify novel sources of scab resistance alleles for apple breeding to develop cultivars with durable apple scab resistance.

Keywords: *Venturia inaequalis*, Disease resistance, Core collection, Differential hosts

Introduction

Disease susceptibility of commercial apple cultivars (*Malus domestica* Borkh.), and the continual emergence of new pathogenic races that overcome resistance genes, are major threats to the apple industry worldwide. Apple scab (causal agent: *Venturia inaequalis* Cke./Wint.) is the most devastating fungal disease of apples in humid areas throughout the world where apple is grown (González-Domínguez et al. 2017). The majority of apple cultivars grown commercially in the USA are susceptible to apple scab. Apple scab lesions on fruit mainly impact their cosmetic appearance, severely limiting their marketability. Growers must apply approximately 12–18 fungicide sprays per growing season to limit quality and yield loss due to apple scab (Peck et al. 2010; MacHardy et al. 2001). Frequent use of fungicides contributes significantly to production costs, and to negative human health and environmental impacts. Apple cultivars resistant

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to scab require fewer fungicide applications, saving on costs and reducing the environmental impact of disease control (Papp et al. 2019; Brown and Maloney 2008; MacHardy et al. 2001). *Malus* accessions and land races maintained in the US national germplasm repository are sources of diverse functional alleles that can be used to breed apple cultivars with enhanced and durable resistance (Byrne et al. 2018). In fact, large-scale screening of germplasm repositories is a common strategy to identify valuable traits for use in breeding for many major crop species (Girichev et al. 2018; Liang et al. 2015; Vasudevan et al. 2014). Conventional commercial apple production is driven mainly by desirable fruit quality traits including taste and shelf life, but development of new apple scab resistant, or tolerant, cultivars might allow reduction of disease management costs, fungicide resistance development, as well as reduce negative environmental and health impacts, and is especially critical for organic and low input production (Koutis et al. 2018; Kellerhals et al. 2004). Unfortunately, the introgression of disease resistance alleles from wild sources into apple cultivars with good fruit quality is a slow and challenging process and so the proportion of scab-resistant cultivars in commercial production remains low (Brown and Maloney 2013).

Genetic resistance to scab in apple is primarily guided by major resistance genes, in a classical gene-for-gene relationship with the *Avr* genes of the pathogen. To date, 20 resistance genes (*Rvi* genes) have been described in *V. inaequalis*, most of which were identified in wild *Malus* accessions and landraces (Bus et al. 2011; Khajuria et al. 2018). Only two of the *Rvi* genes, *Rvi6* (receptor kinase gene) and *Rvi15* (*TIR-NBS-LRR* gene) have been characterized and their functionally validated (Schouten et al. 2014; Jansch et al. 2014). Unfortunately, many of the resistance genes, including the well-characterized *Rvi6* gene, have been overcome by novel virulent races of the scab pathogen (Papp et al. 2019; Parisi et al. 1993, 2004; Xu et al. 2008). A successful apple scab resistance breeding program in the USA between the Universities of Purdue, Rutgers and Illinois (the PRI initiative), used resistance genes from four sources, *M. floribunda* Sieb. ex Van Houtte clone 821 (*Rvi6* and *Rvi7*) (Japanese crabapple), *M. micromalus* Makino (*Rvi5*) (Midget crabapple or Kaido crabapple), *M. domestica* sel. R12740-7A (*Rvi2* and *Rvi4*), and the common apple 'Antonovka' (*Rvi10*, *Rvi17*, polygenic), to develop commercial scab-resistant cultivars and pre-breeding materials. These four genotypes became the foundation for later breeding work worldwide (Crosby et al. 1992). However, most modern scab resistant cultivars carry *Rvi6* resistance from *M. floribunda* 821 (Brown and Maloney 2013).

Monitoring the virulence of pathogen races, as well as understanding the evolutionary and genetic mechanisms responsible for loss of host resistance, are essential both for managing disease resistance and developing durable resistance (Patocchi et al. 2020). In the USA, races 1 to 5 and 9 of *V. inaequalis* have been previously reported to overcome *Rvi1*, *Rvi5* and *Rvi9*, respectively (Beckerman et al. 2009; Durham et al. 1999; Hagan et al. 2000; Shay and Williams 1956; Williams and Kuc 1969), but there is no information regarding races of *V. inaequalis* with an ability to cause disease on apple genotypes with *Rvi11* and *Rvi12* resistance genes (derived from *M. baccata* (L.) Borkh. 'jackii' and 'Hansens baccata #2'). The presence of races 6 and 7, which can infect *M. floribunda* 821, was suggested by Beckerman et al. (2009), but was only recently confirmed by characterization of monosporic isolates of *V. inaequalis* collected from *M. floribunda* 821 (Papp et al. 2019). According to the most recent update from monitoring scab resistance of differential indicator cultivars and accessions in 14 countries, the most promising *R* genes, exhibiting consistent resistance across locations to date, are *Rvi5*, *Rvi11*, *Rvi12*, *Rvi14* and *Rvi15* (Patocchi et al. 2020).

Screening the existing apple germplasm collections for scab resistance can contribute to the identification of additional scab resistance gene resources, and if utilized, eventually to the development of new resistant cultivars with good fruit quality (Papp et al. 2019). The national *Malus* collection at the USDA (United States Department of Agriculture) Plant Genetic Resources Unit (PGRU) is the world's largest apple germplasm repository, with 5004 unique *Malus* accessions growing in the field and 1603 seedlots representing *M. domestica*, 33 *Malus* species, and 15 hybrid species from around the world (Volk et al. 2015a). Approximately 2500 accessions in the collection have been evaluated for a 28-trait descriptor set (Volk et al. 2015a). The collection exhibits broad diversity for a large range of morphological descriptors (e.g., leaf, shoot, flower and bark characteristics), economically important horticultural traits (e.g., tree vigor, shoot traits, ploidy, flowering, fruiting characteristics), disease and pest resistance, and fruit quality traits (Forsline and Aldwinckle 2001, 2003; Harshman et al. 2017; Hokanson et al. 2001; Jurick et al. 2011; Khan and Chao 2017; Luby et al. 1996, 2002; Momol et al. 1999; Myers et al. 2008; Norelli et al. 2013; https://www.ars-grin.gov).

Comprehensive genetic characterization of the entire USDA-PGRU apple collection for disease resistance is laborious and logistically challenging, especially for disease evaluation in the field. Some wild *Malus* accessions of the USDA-PGRU collection, particularly *M. sieversii* (Ledeb.) M.Roem. (Aldwinckle et al. 1997; Hokanson et al. 1997; Volk et al. 2005) and *M. orientalis* Uglitzk. ex Juz. (Volk et al. 2008), have been screened for apple scab resistance, and a considerable number of the accessions

showed resistance to *V. inaequalis* in those studies. In general, and with the exception of a few specifically bred cultivars, *M. domestica* cultivars show a low level of scab resistance (Aldwinckle et al. 1997; Brown and Maloney 2008, 2013). Development of core collections, representing maximum genetic and trait diversity in the genepool of various crop species, has been widely adopted to lower the maintenance costs and evaluation of crop germplasm (Escribano et al. 2008; Liang et al. 2015; Schoen and Brown 1995). To this end, a core collection of 258 individual *Malus* accessions, representing genetic diversity of the whole collection, was established at five field locations in the U.S.A. to assess disease resistance, fruit quality, and horticultural traits (Luby et al. 1996; Potts et al. 2012). With regard to disease resistance, the *Malus* core collection has been evaluated for fire blight resistance in the greenhouse (Khan et al. 2013), but no extensive evaluation has yet been initiated to screen the 258 *Malus* accessions for resistance to apple scab.

Screening accessions in the field is the most direct method to assess scab resistance relevant to production systems. However, for successful infection with the pathogen, not only are a virulent race of *V. inaequalis* and a susceptible host required, but a favorable environment is also needed, so as to satisfy the host/pathogen/environment interactions (Francl 2001). Particularly humid years are conducive to spore germination (Machardy and Gadoury 1989) and offer an excellent opportunity to identify scab resistance in the field; indeed, the identification of *Vf* resistance occurred in such a season (Crosby et al. 1992). The growing season was wet in 2019, and the resulting favorable weather conditions for development of epidemics of scab may have contributed to the development and occurrence of new races of *V. inaequalis* with the ability to infect the previously resistant *M. floribunda* 821 (Papp et al. 2019).

In this study, firstly, we evaluated the scab resistance of 177 diverse *Malus* accessions in the field, including wild species, cultivars, and hybrid selections to identify new sources of scab resistance. Secondly, we assessed scab on a differential host set of ten apple genotypes to monitor the breakdown of resistance for each of the ten known scab resistance genes, and also to monitor the presence of virulent pathogen races in the orchard.

Materials and methods

Plant material

The apple scab resistance reaction types of 177 accessions of the *Malus* core collection were evaluated in the research orchard at Cornell AgriTech, Geneva, New York (42° 52′ 38″ N, 77° 03′ 08″ W). The orchard comprises four replicated blocks of the core collection. The core collection is derived from the USA national *Malus* germplasm repository and includes 27 primary wild *Malus* species and 13 interspecific hybrid species, 61 domestic apple cultivars/landraces and 36 unspecified hybrid selections (Table 1). Most of the hybrid selections were developed by the PRI Initiative and other breeding programs, or are crabapples of unknown parentage. The 177 accessions represent the major part of a core collection of 258 individual *Malus* accessions that was established at five field locations in the U.S.A. to evaluate disease resistance, fruit quality, and horticultural traits (Khan et al. 2013; Luby et al. 1996; Potts et al. 2012). Some trees were lost over time at some orchard locations and were not replaced. The unique Plant Introduction (PI) number of each accession used in this study (Table 1) was obtained from the USDA Germplasm Resources Information Network (GRIN) database (https://www.ars-grin.gov), and can be used to compare accessions evaluated in different studies. In addition, the research orchard includes ten differential host accessions with known apple scab resistance genes to identify previously characterized races of *V. inaequalis*. If a differential host was not available as proposed by Bus et al. (2011), alternative hosts (some with more than one *R* gene) present in the core collection were evaluated as surrogates for that resistance reaction type (Table 2). Information on *Malus* taxonomy for each species was obtained from the GRIN database, which adheres to the *Malus* systematics of Rehder (1915) and Langenfeld (1970).

Orchard maintenance and weather data

Malus accessions in the core collection are grafted on 'M9' rootstocks and are planted in 12 consecutive rows. The 12 rows are divided into 4 blocks (replications) with each replication arranged in 3 rows of trees. Accessions within each replicated block are planted using a randomized block design; in each block there is only one replicate of any accession (i.e., a single tree of each accession per block). Trees have 1.8 m in-row spacing and 3.9 m between-row spacing with a four-wire training system. Trees are approximately 15–20 years old. No pesticides (i.e., insecticides, fungicides, and antibiotics) have been applied in the orchard since 2017 to avoid any possible pathogen, host and pesticide interactions and to observe pathogen isolates and host resistance responses under natural epidemic and selection environments. Trees were occasionally pruned, and a regular mowing schedule was maintained for laneways. The orchard was not fertilized or irrigated during the study period.

A Hobo RX3000 weather station equipped with temperature (Temp) and relative humidity (RH) sensors (Onset Computer Corporation, Bourne, MA) was located approximately 800 m east of the core collection research orchard and was used to collect weather

Table 1 Apple scab resistance of accessions from a *Malus* core collection in a research orchard at Geneva, New York

PI number	Name	*Malus* species	pi number	Name	*Malus* species
Resistant			**Moderately susceptible**		
PI589763	–	angustifolia	PI589820	Prairie Fire	hybrid
PI589838	Hansen's #2	baccata	PI589819	PRI 2050-2	hybrid
PI594110	Jackii	baccata	PI588866	Kerr	hybrid
PI286599		baccata	PI589181	Prima	hybrid
PI589956	Antonovka 172670-B	domestica	PI588991	Bechtel Crab	ioensis
PI590183	Dayton	domestica	PI590015		ioensis
PI588747	Florina	domestica	PI589999		ioensis
PI589962	Jonafree	domestica	PI589932	M0-84	prunifolia
PI594111	Redfree	domestica	PI589390		sikkimensis
PI589726	Britegold	domestica	PI589420	M. hartwigii	sp.
PI588868	–	florentina	PI589958	MA # 4	toringo
PI589933	–	fusca	PI483254		x dawsoniana
PI594105	–	fusca	**Susceptible**		
PI589972	–	halliana	PI594099		asiatica
PI589246	Parkman	halliana	PI594107		asiatica
PI594098	–	hupehensis	PI437055	Flexilis	baccata
PI589522	–	hupehensis	PI588930	Macrocarpa	bhutanica
PI588870	Dolgo	hybrid	PI589170		brevipes
PI589572	E14-32	hybrid	PI589976		coronaria
PI590072	E31-10	hybrid	PI280400	Anna	domestica
PI590070	E7-54	hybrid	PI589596	Calville Blanc	domestica
PI589794	PRI 1754-2	hybrid	PI588848	Cortland	domestica
PI589807	PRI 1773-6	hybrid	PI588853	Cox's Orange Pippin	domestica
PI589792	PRI 1850-4	hybrid	PI589024	Crimson Beauty	domestica
PI589777	PRI 1918-1	hybrid	PI589841	Delicious	domestica
PI588992	White Angel	hybrid	PI590179	E.8	domestica
PI589570	E36-7	hybrid	PI280401	Ein Shemer	domestica
PI590008	–	ioensis	PI588842	Empire	domestica
PI594097	–	kansuensis	PI588785	Esopus Spitzenburg	domestica
PI589955	–	micromalus	PI392303	Gala	domestica
PI594096	–	micromalus	PI590184	Golden Delicious	domestica
PI588933	–	prattii	PI588880	Granny Smith	domestica
PI589832	Xanthocarpa	prunifolia	PI589469	Haralson	domestica
PI594102	–	prunifolia	PI588841	Idared	domestica
PI588761	–	sargentii	PI589441	Ingol	domestica
PI594094	–	toringo	PI589122	Kimball McIntosh 2-4-4-4	domestica
PI589395	–	tschonoskii	PI589053	Lady	domestica
PI588757	–	x hartwigii	PI588998	Marshall McIntosh	domestica
PI588959	–	x magdeburgensis	PI589486	Murray	domestica
PI589415	Hoopesii	x platycarpa	PI588872	Northern Spy	domestica
PI588825	Robusta 5	x robusta	PI589478	Novosibirski Sweet	domestica
Moderately resistant			PI588798	Rambo-Red Summer	domestica
PI588960	Rockii	baccata	PI589255	Redspur Delicious	domestica
PI322713	Mandshurica 2330	baccata	PI483257	Reinette Simirenko	domestica
PI588943	Liberty	domestica	PI589520	Rhode Island Greening	domestica
PI589490	Trent	domestica	PI588850	Rome Beauty Law	domestica

Table 1 (continued)

PI588806	Chisel Jersey	domestica	PI589006	Spokane Beauty	domestica
PI107196	Antonovka 1.5 pounds	domestica	PI588955	Sweet Delicious	domestica
PI588838	Nova Easygro	domestica	PI589434	Viking	domestica
PI589975	–	fusca	PI590186	Wijcik McIntosh	domestica
PI589941	–	fusca	PI588778	Virginiagold	domestica
PI590071	E29-56	hybrid	PI589491	Korichnoe Polosatoje	domestica
PI590085	PRI 1176-1	hybrid	PI589913	Dorsett Golden	domestica
PI589812	PRI 2377-1	hybrid	PI589645	Winter Majetin	domestica
PI589790	PRI 1484-1	hybrid	PI588981	Mollie's Delicious	domestica
PI589775	PRI 2382-1	hybrid	PI589845	Smith Jonathan	domestica
PI589946	PRI 1732-2	hybrid	PI588772	Monroe	domestica
PI589795	PRI 2482-100	hybrid	PI246464	James Grieve (Red Rosamund strain)	domestica
PI589785	PRI 1346-2	hybrid	PI588844	Fuji Red Sport Type 2	domestica
PI589805	Co-op 15	hybrid	PI590185	Jonathan	domestica
PI588883	Demir	hybrid	PI589827	821	floribunda
PI589776	PRI 1316-1	hybrid	PI589824	Jonsib Crab	hybrid
PI590069	E7-47	hybrid	PI589791	PRI 1279-9	hybrid
PI588944	Calva	kansuensis	PI589780	PRI 384-1	hybrid
PI594092	–	micromalus	PI589829	PRI 333-9	hybrid
PI594095	–	orientalis	PI589571	E11-24	hybrid
PI589816	19651	prunifolia	PI589786	PRI 77-1	hybrid
PI589421	M. rockii	sp.	PI588824	Almey	hybrid
PI589382	–	sylvestris	PI590079	PRI 1312-6	hybrid
PI369855	–	sylvestris	PI588804	Kansas K14	hybrid
PI589749	–	toringo	PI589380		kirghisorum
PI589384	–	transitoria	PI590043		kirghisorum
PI589003	Korea	x robusta	PI588753		mandshurica
PI271831	Vilmorin	yunnanensis	PI589753		micromalus
PI589758	Veitchii	yunnanensis	PI594101		orientalis
Moderately susceptible			PI594109	Microcarpa	prunifolia
PI589727	–	angustifolia	PI589930	Nagano	prunifolia
PI589869	–	asiatica	PI594103	Inuringo	prunifolia
PI589393	–	bhutanica	PI323617		pumila
PI588995	Antonovka Kamenichka	domestica	PI594106		pumila
PI588835	Burgundy	domestica	PI594104		sieversii
PI589970	Petrel	domestica	PI594100		spectabilis
PI589894	Keepsake	domestica	PI619168		sylvestris
PI588859	Yellow Transparent	domestica	PI589222	Arnold Crab	x arnoldiana
PI123989	Emilia	domestica	PI589253	Carmine Crab	x atrosanguinea
PI104727	Irish Peach	domestica	PI589383	Persicifolia	x robusta
PI589648	Rosemary Russet	domestica	PI589391		x soulardii
PI588837	Gravenstein Washington Red	domestica	PI588922	Yellow Autumn Crab	x sublobata
PI589789	PRI 1744-1	hybrid	PI590174	Novole	x sublobata
PI437057	Roberts Crab	hybrid	PI589840	Calocarpa	x zumi

Grouping of accessions into different classes is based on a visual assessment of the scab response type on visible leaves throughout the tree canopy on each tree in four replicated blocks and three sampling dates in 2018 and 2019. Assessments were based on an ordinal scale developed by Chevalier et al. (1991). Plant Introduction (PI) number of each accession is provided according to the USDA Germplasm Resources Information Network (GRIN)

data in 2018 and 2019. Temp and RH readings were collected at 5-min intervals and transmitted in real-time to the HOBO RX3000 base station, which uploaded data at 15-min intervals to HOBOlink. Datasets were generated in HOBOlink for download, with hourly summarizations and subsequent analysis. Wet periods (RH > 90%) represented infection risk and were used to calculate Mills periods, based on the Temp and wet

Table 2 Severity of apple scab at two timepoints in 2019 on a scab differential host set in the research orchard at Geneva, New York

Differential host[a]	Host name	PI number	*R* gene	Severity (1–9, July)	Severity (1–9, August)
h0	Gala	392303	–	5	6
h1	Golden Delicious	590184	*Rvi1*	7	7
h2	TSR34t15 (syn. PRI 384-1)	589780	*Rvi2*	4	4
h3	*Malus* × 'Geneva'	589079	Rvi3.1, Rvi3.2, Rvi3.3	3	4
h4	TSR33t239	N/A[b]	*Rvi4*	5	5
h5	OR45T132 (syn. PRI 333-9)	589829	*Rvi5*	4	4
h6	Priscilla	589965	*Rvi6*	1	1
h7	*Malus floribunda sel. 821*	589827	*Rvi6, Rvi7*	4[c]	4[c]
h9	*Malus* × 'Dolgo'	588870	*Rvi9*, unknown	4	4
h11	*Malus baccata* 'jackii'	594110	*Rvi11*, unknown	1	1
h12	*Malus baccata* 'Hansens baccata #2'	589838	*Rvi12*	1	1

The scab severity within the tree canopy was visually assessed in four replicate trees of each accession using a 9 point scale described by Lateur and Populer (1994) and adapted by Patocchi et al. (2009), taking the most severely infected tree of each accession as the representative sample. These differential host accessions have known apple scab resistance genes (Bus et al. 2011) corresponding to specific races of *V. inaequalis*. Plant Introduction (PI) number of each accession is provided according to the USDA Germplasm Resources Information Network (GRIN)

[a] Differential apple hosts carrying specific *Rvi* scab resistance genes as described in Patocchi et al. (2020)

[b] Not available in the USDA-PGRU GRIN database

[c] Scab severity reported by Papp et al. (2019)

period duration according to MacHardy and Gadoury (1989).

Assessment of apple scab symptoms

Symptoms of apple scab on the 177 *Malus* accessions and the 10 differential apple host genotypes were evaluated three times a year in June, July, and August in 2018 and 2019. Evaluations consisted of a careful examination of the visible leaves in the tree canopy of each of the 177 trees and 10 differentials, in each of the 4 replicated blocks. The scab evaluations were used to ascertain the resistance response types of each of the accessions in the orchard, using a previously developed rank ordering of scab symptoms (Chevalier et al. 1991). The classes of the ordinal scale are as follows:

0—no symptoms; 1—pin point pits; 2—chlorotic lesions; 3a—necrotic and some chlorotic lesions, very weak sporulation; 3b—clearly sporulating chlorotic and necrotic lesions; and 4—abundantly sporulating lesions covering most of the leaf area. Based on the symptom classes we distinguished four response categories: 1—Resistant (symptom class: 0, 1, 2), 2—moderately resistant (3a), 3—Moderately susceptible (3b), 4—susceptible (4).

In addition, the 10 differential host accessions in the four replicated orchard blocks were evaluated for scab severity in early July and August of 2019. The most severely infected tree of each host accession in the four replicated blocks was used to represent the accession. The scab severity within the tree canopy was visually evaluated using a 9 point ordinal scale described by Lateur and Populer (1994) and adapted by Patocchi et al. (2009): 0—no observation (missing plant); 1—no visible scab lesions; 2—one or very few scab lesions detectable on close scrutiny of the tree (0–1%); 3—Immediately apparent scab lesions, generally clustered in a few parts of the tree (1–5%); 4—intermediate; 5—numerous scab lesions widespread over a large proportion of the tree (±25%); 6—intermediate; 7—severe symptoms of scab with half of the leaves severely scabbed exhibiting multiple lesions (±50%); 8—intermediate (±75%); or 9—foliage of tree completely affected with (nearly) all the leaves severely diseased by multiple scab lesions (>90%).

Data analyses and visualization

Statistical analyses were performed to evaluate the difference between the weather conditions of the 2 years, and to test differences in scab resistance of the accessions. The scab resistance reaction type data collected at three time points in 2018 and 2019 were used to assess scab susceptibility of each of the accessions. Scab resistance reaction type and severity data collected over 2 years for the differential hosts with ten known scab resistance genes were used to assess whether any local races of *V. inaequalis* were able to overcome the genetic resistance in hitherto resistant differentials and to identify novel sources of apple scab resistance. Results of daily RH and Temp data from April to October and scab

resistance responses of accessions/*Malus* taxonomy groups for each species were visualized in R version 3.6.2 (R Core Team 2020) using the inbuilt functions and the *ggplot2* package (Wickham 2016). The effect of different genotypes and different time points within and across years on the disease severity inferred from the scab resistance reactions was explored using an ordinal logistic regression model in IBM SPSS Statistics v.25.0 (Arkmonk, NY). Furthermore, the total number of plants in each of the four categories of resistance response symptom classes for each month (June, July and August) in 2018 and 2019 and the corresponding weather variables were used to perform principal component analysis (PCA) analysis to study the effect of weather variables on disease susceptibility. The PCA results were explored graphically using biplots with the packages *FactoMineR* (Husson et al. 2020) and *factoextra* (Kassambara and Mundt 2017) in R version 3.6.2. Weather variables used included: average RH (RHave), minimum RH (RHmin), maximum RH (RHmax), average temperature (Tave), minimum temperature (Tmin), and maximum temperature (Tmax) for June, July and August 2018 and 2019. Pearson's correlation analysis among these variables was performed in R version 3.6.2. A chi-square test was performed to evaluate relationship among *Malus* taxonomic groups and scab severity.

Results

Impact of weather conditions on apple scab severity

In 2019, a higher proportion of the *Malus* core collection trees were infected with scab, which reached a plateau of approximately 50% of all the trees in the orchard, in contrast to 25% in 2018 (Figs. 1 and 2). The ordinal logistic model showed significant ($P < 0.0001$) difference among the genotypes and the six timepoints in apple scab susceptibility. According to the dispersion of Mills periods across the two study years, 2019 experienced conditions favorable to infection by apple scab 2 weeks earlier (data not shown). During the early vegetative phase of growth, both average Temp and RH (%) were higher in 2019 compared to in 2018 (Fig. 3). Later in the season, the relative difference in temperature between the 2 years shifted, but was close to the 16 to 23.9 °C optimum for scab development. The high Temp peaks in June and July of 2018 were > 32 °C, higher than the more consistent daily temperatures experienced in 2019. The average monthly RH was higher in April, May, and July in 2019, and RH was > 90% more often throughout the whole season in 2019, providing more suitable conditions for spore germination of *V. inaequalis*.

The PCA biplot showed a strong positive association among RHave, RHmin and Tmin, and negative association between RHmax and Tmax (Fig. 4). The variables RHave and RHmin, RHave and Tmin, and RHmin and

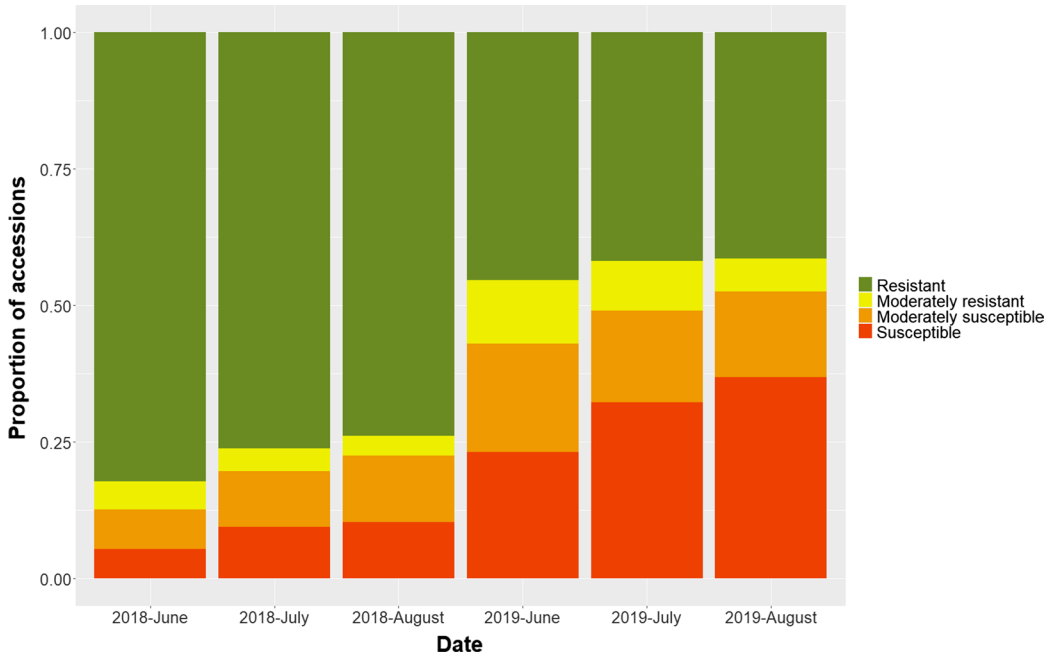

Fig. 1 Proportion of resistance reaction type classes observed on each of six evaluation dates during the growing seasons of 2018 and 2019 in the *Malus* germplasm core collection in the research orchard at Geneva, New York. Resistance categories were assessed as proposed by Chevalier et al. (1991). The orchard was not sprayed with pesticides

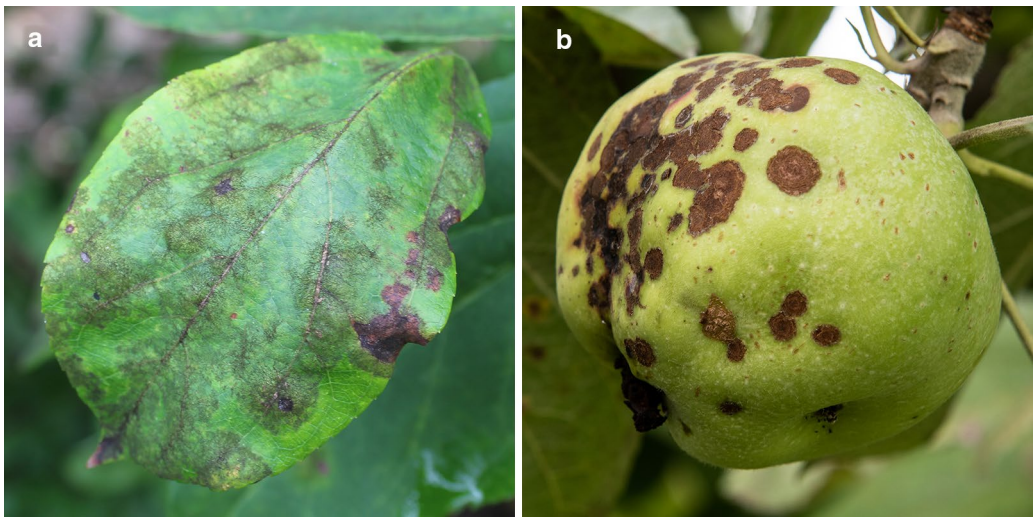

Fig. 2 Severe apple scab symptoms on 'Calville Blanc' apples (**a**) leaves and (**b**) fruit in the *Malus* core collection in the research orchard at Geneva, New York

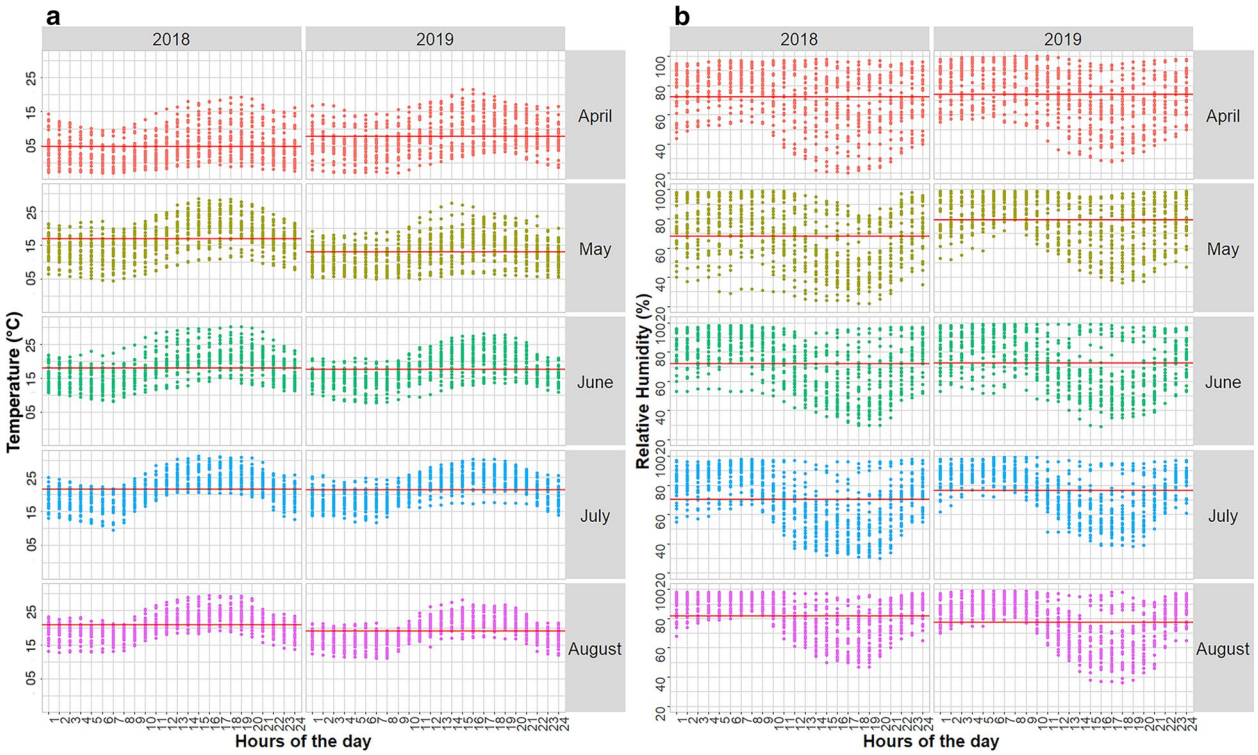

Fig. 3 Daily dispersion of (**a**) temperature (°C) and (**b**) relative humidity (%) from April to August in 2018–2019, at the same location as the *Malus* germplasm core collection at Geneva, New York. Different colors indicate different months. The red line shows (**a**) the mean temperature, and (**b**) the mean relative humidity for each of the months

Tmin showed positive correlations (r) of 0.96, 0.86 and 0.93, respectively, whereas RHmax and Tmax showed a negative correlation (r) of − 0.61. The first two PCs (principal components) explained 86.6% of the variation; PC1 and PC2 explained 53.6% and 33% of the variation, respectively. Apple scab susceptibility was found to be

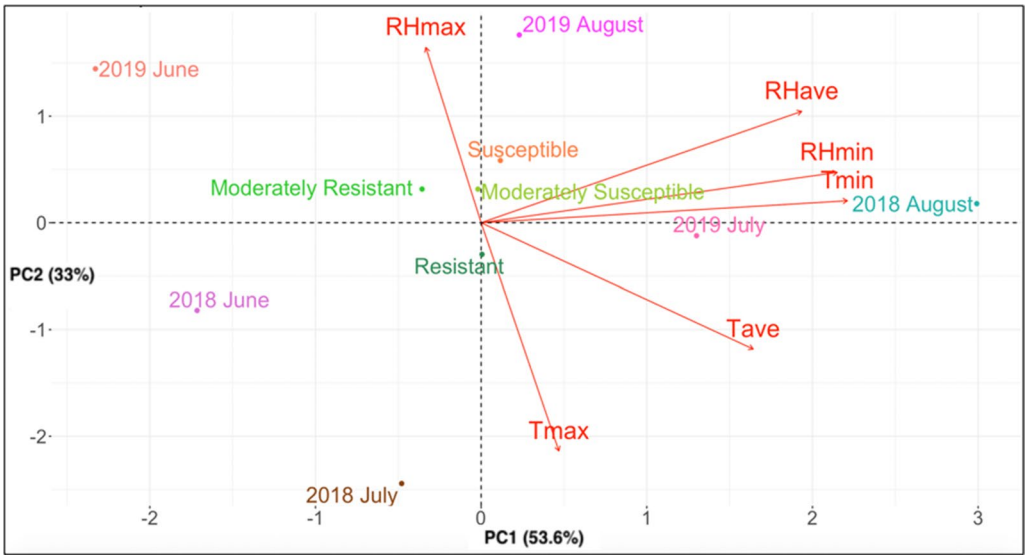

Fig. 4 PCA biplot showing PC1 and PC2 to depict the relationship between different weather parameters and apple scab severity (resistance reaction type) for the six dates when scab was evaluated. The number of plants in the *Malus* germplasm core collection in each of four categories of symptom classes: Resistant, Moderately resistant, Moderately susceptible, and Susceptible were counted in June, July and August of 2018 and 2019, and used to perform principal component analysis (PCA) using the package *FactoMineR* (Husson et al. 2020) and *factoextra* (Kassambara and Mundt 2017) in R version 3.6.2 (R Core Team 2020). Weather variables are: average relative humidity (RHave), minimum relative humidity (RHmin), maximum relative humidity (RHmax), average temperature (Tave), minimum temperature (Tmin), and maximum temperature (Tmax)

influenced by RHmax, RHave, RHmin and Tmin, whereas apple scab resistance was found to be influenced by Tmax as depicted by the location of RHmax in relation to the moderately susceptible accessions, RHave, RHmin, Tmin, and the susceptible accessions, and Tmax and the resistant accessions in the same quadrant of the PCA biplot i.e. quadrant II, I and IV of the PCA biplot, respectively. The presence of RHmax and susceptible accessions, and Tmax and resistant accessions in close proximity to each other in the PCA biplot shows strong association of RHmax and scab symptom development, and Tmax and disease resistance respectively (Fig. 4).

Scab severity on the differential set

The indicator accessions with ten known scab resistance genes were used to monitor the severity of scab infection in relation to races of *V. inaequalis* present in the orchard (Table 2). 'Gala' showed heavy scab infection in both years. Scab severity on 'Golden Delicious', carrying *Rvi1,* was even higher (class 7) compared to severity on the susceptible control. Differential hosts 2 (TSR34t15), 3 (*M.* × 'Geneva'), 4 (TSR33t239), 5 (OR45T132) and 9 (*M.* × 'Dolgo') were all severely diseased with scab, indicating the presence of races 1 to 5 and race 9. Scab severity was as high as class 4, except for host differential indicator for race 4, which was rated in scab severity class 5 by the end of the season. *M. baccata* 'Jackii' (indicator for race 11) and 'Hansens baccata #2' (indicator for race 12) were free of scab. Severe scab was observed on *M. floribunda* 821, the source of *Rvi6* and *Rvi7* resistance, as reported earlier by Papp et al. (2019), but 'Priscilla' (*Rvi*6) was free of scab symptoms. Overall, resistance response types were consistent over the period of assessment, with only slight differences in severity.

Sources of novel scab genetic resistance in the core collection

Of the 177 *Malus* accessions evaluated for apple scab symptom, a total of 49, 17, 32, and 79 accessions were free of scab or resistant (ordinal scale classes 0, 1, 2), had weak sporulation (3a), had well-developed sporulating lesions (3b), or were completely susceptible (4), respectively (Table 1; Additional file 1: Table S1). The 49 resistant accessions are mostly primary *Malus* species (46.9%), hybrids from breeding programs (22.4%), secondary *Malus sp.* (14.3%), and *Rvi6* resistant cultivars (12.2%); there were two apple 'Antonovka' landraces (4%). In contrast to the large number of resistant accessions among the primary apple species, no modern domestic cultivar lacking a known major resistance gene was found to be completely free of scab. In the most susceptible category (n = 79), 51.8% were domestic cultivars. Out of 61 *M. domestica* accessions included in the study, 8 were resistant to apple scab ('Antonovka 172670-B', 'Antonovka 43470 lb', 'Britegold', 'Dayton', 'Florina', 'Jonafree', 'Liberty', and 'Redfree'). Most of these accessions with scab

resistant phenotypes can be traced back to PRI breeding materials and are considered to have *Rvi6* resistance from *M. floribunda* 821. Sporulation of scab lesions was noticed on *Rvi6* cultivars 'Prima' and 'Nova Easygro' and has been reported previously (Papp et al. 2019). In addition, PRI cultivars 'Murray' (*Rvi5*), 'Trent' (*Rvi6*) and 'Viking' were found to show scab symptoms. Only 5 of the 19 hybrid selections listed by their PRI codes did not show symptoms during the 2 years. The selections PRI 333-9 (syn. OR45T132, *Rvi5*) and PRI 384-1 (syn. TSR34T15, *Rvi2*) were both severely scabbed. Besides the PRI derivates, two cultivars: 'Demir' and 'Chisel Jersey', were evaluated as moderately resistant to scab. Traditional heritage cultivars including 'Gravenstein Washington Red' and 'Irish Peach', or 'Burgundy' had less severe symptoms compared to 'McIntosh', 'Granny Smith', 'Gala', or 'Golden Delicious'.

The highest number of scab infected accessions are in the *Malus* section. In August 2019, scab severity was the highest in the *Malus* section at all time points; approximately 81% of the genotypes in the *Malus* section showed scab susceptibility (Additional file 1: Table S1). The percentage of scabbed genotypes for the interspecific hybrids was approximately 41%, and for the sections Chloromeles, Gymnomeles, and Sorbomalus was 35%, 28%, and 18% of trees, respectively (Fig. 5). No completely susceptible accession was identified in the sections Sorbomalus and Dyconiopsis. However, the section Dyconiopsis, comprised only one accession with 3 samples, which showed moderate susceptibility in 2018, but not in 2019. Scab resistance differed significantly among six taxonomic groups ($\chi^2_{(d.f.\ 4)} = 40.365$, $p < 0.001$). Although the proportion of trees with apple scab increased from 2018 to 2019, this did not affect the relative differences between the scab susceptibilities of the taxonomic groups.

Discussion

Detailed and systematic screening of diverse *Malus* germplasm can identify donor accessions for sources of novel and durable apple scab resistance. We have identified potential new sources of scab resistance among *M.*

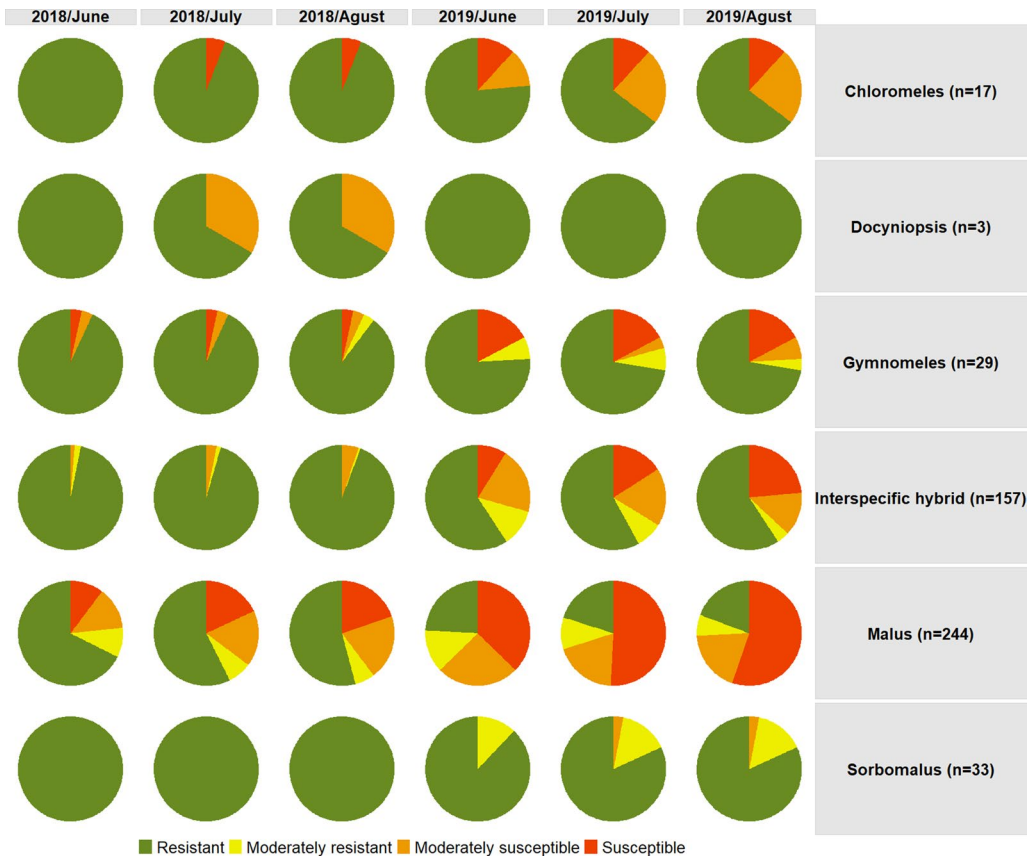

Fig. 5 Proportion of infected trees of each accession according to their taxonomic affiliation (obtained from the USDA GRIN) at six timepoints during 2018 and 2019 in the *Malus* germplasm core collection in the research orchard at Geneva, New York. Symptom classes (resistance response types) were assessed as proposed by Chevalier et al. (1991). Numbers provided in parenthesis refers to the number of trees in the section

domestica cultivars and crabapples. Resistant and moderately resistant accessions are promising for use in future genetic studies to identify novel sources of scab resistant alleles for apple breeding (Patocchi et al. 2020; Papp et al. 2019). Domestic cultivars 'Demir' and 'Chisel Jersey' were moderately resistant. Although occasional weak sporulation was observed on some of the trees, the sporulation was slight and the severity low enough to preclude posing any economic threat to production. In addition, we noticed that both 'Demir' and 'Chisel Jersey' are late season and there is the possibility that they escaped a high-risk infection period. 'Demir' is a Turkish fresh eating cultivar, while 'Chisel Jersey' is a cider cultivar from the United Kingdom (UK). Many of the crabapples with unknown resistance were free of scab, including accessions of unknown hybrid species, breeding materials and *Malus* species. The majority of *R* genes are derived from small-fruited crabapples: *Rvi2* and *Rvi4* from *M. pumila* R12740-7A, *Rvi5* from *M.* × *atrosanguinea* Schneid. sel. 804 and *M. micromalus* 245–38, *Rvi6* and *Rvi7* from *M. floribunda* 821, *Rvi8* from *M. sieversii* GMAL4302-X8, *Rvi11* from *M. baccata* 'jackii', *Rvi12* from *M. baccata* 'Hansen's 2#' and *Rvi9* from *M.* × 'Dolgo', possibly a clone of *M. baccata* or *M. prunifolia* (Willd.) Borkh. (Bus et al. 2011). We lack molecular and genomic data to characterize the genetic basis of the resistance of many of these promising accessions, although it is possible that these resistances were due to already-described major genes or by polygenic quantitative resistance. Novel single gene-based resistance can be easier to characterize and provide new opportunities for apple breeding. At the same time new technologies including biotechnology, genomics, marker assisted selection and novel breeding methods might make polygenic resistance sources more accessible and reliable for apple breeding in the future.

We observed the breakdown of major resistance genes *Rvi1* to *Rvi7* and *Rvi9* in the research orchard. The *V. inaequalis* races 1, 7 and 9 have all been reported previously from the U.S.A. (Beckerman et al. 2009; Durham et al. 1999; Papp et al. 2019; Shay and Williams 1956; Williams and Kuc 1969). No scab was observed on the differentials of race 11 and 12, although of these, only host 11 (alongside the host for race 15, which was not included in the study) were assigned as 'not overcome' by a recent update on worldwide race distributions (Patocchi et al. 2020). In the case of hosts for races 2 (PRI 384-1) and 5 (PRI 333-9, 'Murray', *Malus sp.* 'Prairie Fire'), all other genotypes screened that possessed known *R* genes have confirmed breakdown; in the case of *Rvi6,* many cultivars remained resistant (e.g. 'Liberty', 'Florina'). It should be noted that the only apple cultivars with good fruit quality, and that have scab resistance are those with the *Rvi6* gene. We do not yet know why *Rvi6* cultivars retain their resistance when the original host source of the *Rvi6* resistance can be infected by *V. inaequalis*. Investigating the reason why infection of *Malus floribunda* 821, the source of *Rvi6* resistance, is possible, but infection of descendant cultivars is not will be of value for informed development of scab resistant cultivars in the future.

In our study, we have identified a clear relationship between the taxonomic affiliation and the scab susceptibility of *Malus* germplasm. The relationship might reflect host frequency-based selection on the pathogen, hypothesizing that scab susceptibility of wild species is directly related to their genetic proximity to the domesticated apple. The domestication of apples started in Central Asia, where the primary progenitor, *M. sieversii* exists in large natural populations. Congruent with this host distribution, *V. inaequalis* populations infecting domesticated apples originated from Central Asia and coevolved with *M. sieversii* during the domestication process (Gladieux et al. 2008, 2010). Populations of the pathogen tend to show distinct genetic structure related to their original *Malus* host species, and the breakdown of resistance genes derived from wild *Malus* species might be caused by divergent pathogen populations emerging from wild apple reservoirs, as has been demonstrated in the case of *Rvi6* resistance (Gladieux et al. 2010; Lemaire et al. 2016; Leroy et al. 2016; Michalecka et al. 2018). *M. sieversii* accessions (including the accession of *M. kirghisorum* syn. *M. sieverii var. kirghisorum*) were susceptible to apple scab in our study. There is substantial genetic evidence that the European wild apple *M. sylvestris*, *M. orientalis* with gene centers to the west of Central Asia, as well as *M. baccata* with gene centers in East Asia, have hybridized with domestic apple during the domestication process (Cornille et al. 2012, 2014; Duan et al. 2017; Volk et al. 2015b). Overall, accessions of *M. domestica* and *M. sieversii*, two closely related species, had considerably more severe scab compared to the accessions of the other wild *Malus* species. Despite this finding, the inoculum of *V. inaequalis* from the *Malus* core collection research orchard might simply not be diverse enough to reflect larger scale trends and might represent races specialized to domestic cultivars. Larger-scale genetic studies and genome-based analysis of local isolates will contribute to understanding the pathogen in relation to host specificity patterns in the *Malus-Venturia* pathosystem.

A consequence of modern production systems with large acreage of monocultures could facilitate specialization of pathogen strains on particular cultivars, the build-up of large populations on uniform host populations with rapid dissemination of the new strain (McDonald and Stukenbrock 2016). The sexual and asexual phases of *V. inaequalis* can allow it to evolve rapidly and in the context of modern high-density

apple orchards, it has the ability to quickly overcome genetic resistance in apples. Therefore, it is critical to continue to identify and characterize new sources of both qualitative and quantitative scab resistance and pyramid multiple resistance sources in order to develop apple cultivars with durable scab resistance. The scab resistance screening data from this study can be combined with previous assessments for fire blight resistance, fruit quality, and horticultural traits (Khan et al. 2013; Luby et al. 1996; Potts et al. 2012) available for the majority of the accessions in the *Malus* core collection to identify potential sources for introgression of multiple traits for cultivar development. At the same time, it is also important to understand the relationship between the evolutionary potential of *V. inaequalis* and current disease management practices for enhancing the durability of the resistance genes. Disease management practices to decrease population sizes of the pathogen, limiting production of sexual inoculum, may also contribute to reducing the pathogen's evolutionary potential (McDonald 2015).

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s43170-020-00017-4.

Additional file 1: Table S1. Apple scab resistance response type of 177 *Malus* accessions in four blocks (replications) across six sampling dates in 2018 and 2019. Resistance response type was evaluated in a research orchard at Geneva, New York by visually assessing scab severity on single leaves throughout the visible tree canopy of single trees/accessions in each replicated block. Plant Introduction (PI) number of each accession is provided according to the USDA Germplasm Resources Information Network (GRIN).

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Authors' contributions
AK designed the experiment, supervised the research and revised the manuscript. DP and LG collected the apple scab data in 2018 and 2019 respectively. DP analyzed the data and wrote the manuscript, RT helped with statistical analysis, DO supported weather data collection. All authors read and approved the manuscript.

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Not applicable.

Ethics approval and consent to participate
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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