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Field Evaluation of Potato Genotypes for Resistance to Powdery Scab on Tubers and Root Gall Formation Caused by *Spongospora subterranea*

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Abstract *Spongospora subterranea* causes root galls and powdery scab on potato tubers (*Solanum tuberosum* L.). Host resistance represents an economically suitable and long term approach for the management of the disease; however, the relationship between root and tuber symptoms may vary across potato genotypes. To assess susceptibility differences among genotypes, 30 potato cultivars and 83 advanced clones with varying skin type (market class) were evaluated for powdery scab and root gall formation. Five field experiments were conducted during 2011 and 2012 on naturally infested soils in Minnesota and North Dakota. Differences among genotypes in the degree of susceptibility to tuber and root symptoms were observed ($P < 0.001$, $n = 33$ to 80). Higher powdery scab pressure ($P < 0.001$, $n = 90$) was observed in North Dakota locations across years. Environmental conditions influenced the formation of root galls and the expression of powdery scab, with greatest variability among white- and red-skinned genotypes. Under high disease pressure, the estimates of broad-sense heritability for powdery scab incidence and severity were 0.76 and 0.63, respectively. Across environments, russet-skinned genotypes resulted in less disease on tubers, but yielded similar levels of root galls as red-skinned genotypes. Tuber scab and root gall formation indices were significantly associated ($r = 0.42$, $P < 0.001$, $n = 80$); however, high levels of disease in roots were observed in genotypes ranked resistant to powdery scab. Cultivars Dakota Trailblazer, Dakota Russet and Karu ranked highly resistant, whereas Shepody, Kennebec and Red LaSoda were highly susceptible to both phases of the disease. Cultivar selection is highly recommended for disease management.

Resumen *Spongospora subterranea* causa sarna polvorienta y agallas en tubérculos y raíces de papa (*Solanum tuberosum* L.). La resistencia del hospedante representa una alternativa económica y duradera para el manejo de la enfermedad; sin embargo, la relación entre síntomas en raíces y tubérculos puede variar entre genotipos de papas. Con el fin de evaluar diferencias en susceptibilidad a la sarna polvorienta y la formación de agallas entre genotipos, 30 cultivares de papa y 83 clones avanzados con diferentes tipos de piel (clase comercial) fueron evaluados. Durante los años 2011 y 2012 se llevaron a cabo un total de cinco experimentos de campo en Minnesota y Dakota del Norte. Diferencias en el grado de susceptibilidad a la sarna polvorienta y la formación de agallas fueron observadas entre genotipos de papa ($P < 0.001$, $P < 0.001$, $n = 33$ a 80). En Dakota del Norte, la presión de la sarna polvorita fue mayor a través de los años ($P < 0.001$, $n = 45$). Las condiciones ambientales influenciaron la formación de agallas y la expresión de la sarna polvorienta, observándose la mayor variabilidad en cultivares de piel blanca y roja. Bajo alta presión de enfermedad, los estimados de heredabilidad en sentido amplio para la incidencia y severidad de la sarna polvorienta fueron de 0.76 y 0.63, respectivamente. A través de los ambientes, los genotipos de piel arrosetada desarrollaron poca enfermedad en tubérculos, pero los niveles de agallas radicales fueron similares a los observados en genotipos de piel roja. La correlación entre índices de sarna en tubérculos y formación de raíces fue significativa ($r = 0.42$, $P < 0.001$, $n = 80$); sin embargo, altos niveles de enfermedad en raíz fueron observados en genotipos con resistencia a sarna polvorienta. Los cultivares Dakota

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Trailblazer, Dakota Russet y Karu fueron catalogados altamente resistentes, mientras Shepody, Kennebec y Red LaSoda fueron altamente susceptibles a ambas fases de la enfermedad. La selección del cultivar se recomienda para el manejo de la enfermedad.

Keywords Plasmodiophorids · Potato cultivar · Advanced clones · Obligate parasite · Soil-borne · Tuber-borne

Introduction

Spongospora subterranea (Wallr.) Lagerh. is a biotrophic protozoan pathogen (Cercozoa, Plasmodiophorida) of solanaceous crops. On potato, *S. subterranea* causes root galls and powdery scab on tubers (Cavalier-Smith 1998; Harrison et al. 1997; Neuhauser et al. 2010). Members belonging to the Plasmodiophorida group develop multiple somatic structures including multinucleated plasmodia, zoosporangia, biflagellate zoospores and resting spores (Braselton 1995, Hernandez Maldonado et al. 2013). The pathogen life cycle consists of a sporangial (primary) and a sporogenic (secondary) phase. Initial infections of the epidermal root cells, stolons and young tubers develop sporangial zoosporangia from which short-lived zoospores emerge. Repeated infection cycles result in a polycyclic nature of the disease (van de Graaf et al. 2000). During the sporogenic phase, *S. subterranea* undergoes cruciform division and meiosis resulting in the development of resting spores arranged in aggregates (sporosorus). This phase is accompanied by the hyperplasia and hypertrophy of the host cortical cell; promoting the formation of root galls and pustules on tubers. When mature, hypertrophied cells burst, causing lesions and releasing masses of sporosori (Merz and Falloon 2009).

Resting spores of *S. subterranea* are highly resistant to environmental stresses and can remain viable for over 10 years (Merz and Falloon 2009). Prediction models estimate a high risk of developing powdery scab in fields in which potato is grown once at least every 5 years (Sparrow et al. 2015). Lesions on tubers are responsible for the spread of the pathogen to other fields (Merz and Falloon 2009). Additionally, resting spores borne on asymptomatic tubers can induce the formation of root galls in the absence of soil-borne inoculum (Tegg et al. 2015). The severity of powdery scab, as well as the amount of inoculum borne on tubers of the cultivars Innovator and Russet Burbank, were shown to be strongly associated with formation of root galls (Tegg et al. 2015).

Powdery scab is a quality limiting disease (Wale 2000). In the US, a lot can be downgraded when tubers have >5 % surface coverage, and lots with severity >25 % are considered non-marketable (Houser and Davidson 2010; USDA 2014a). However, the effect of powdery scab and root gall formation on tuber yield appears to be small, or at least not negative (Johnson and Cummings 2015; Wale 2000). Root infection by the pathogen is generally accompanied by cell necrosis, reduction of nutrient uptake and water absorption (Lister et al. 2004). Under controlled conditions, the infection by *S. subterranea* was shown to reduce tuber yield; the decrease in yield and tuber weight was more pronounced on healthy tubers (Shah et al. 2005, 2012). The detrimental effect of infection by the pathogen is also likely to interact with the potato cultivar and compounded with the damage caused by other soil-borne pathogens (e.g. *Colletotrichum coccodes*; Johnson and Cummings 2015; Merz and Falloon 2009). Furthermore, *S. subterranea* is the vector of the *Potato mop-top virus* (PMTV; Jones and Harrison 1969), which causes internal necrotic lesions rendering tubers undesirable for consumption or processing (Davey et al. 2014). Recent reports demonstrated a significant association between the incidence of PMTV-induced tuber necrosis and the number of galls per plant ($r = 0.52$, $P = 0.05$), as well as the incidence of powdery scab on tubers ($r = 0.62$, $P = 0.02$; Domfeh et al. 2015).

In the field, the occurrence and degree of disease development is drastically limited by environmental conditions. Cool soil temperatures (10 to 20 °C) are conducive for symptom development (de Boer et al. 1985). Likewise, constant levels of high soil moisture (> −0.01 bars) are more favorable than fluctuating regimes (van de Graaf et al. 2005, 2007). Conducive levels of soil moisture can be provided by irrigation and rainfall (Johnson and Cummings 2015). Soil characteristics (i.e. texture, structure) accounting for water movement and gas interchange are likely to influence disease expression. Powdery scab can occur on a variety of soil textures, however, the disease seems to be more prevalent in organic and sandy soils (Brierley et al. 2009; Tuncer 2002; van de Haar 2000).

Host resistance highly influences disease development, yet most of the commercially available grown cultivars are susceptible to some degree (de Boer 1991; Kirkham 1986; Merz et al. 2012). In field experiments conducted in Peru to assess susceptibility to powdery scab, 50 out of 467 potato genotypes evaluated were reported to have some level of resistance to the disease (Torres et al. 1995). In New Zealand, 99 cultivars and 13 breeding lines were evaluated for their susceptibility to powdery scab, and it was observed that resistance followed a continuum from very resistant to very susceptible, suggesting a trait controlled by multiple genes (Falloon et al. 2003). Elsewhere, tuber resistance has been described to be inherited in an additive manner (Wastie 1991). Susceptibility to root gall formation is likely to be governed by a number of genes similar to the tuber phase of the disease; however, the degree of association between resistance to powdery scab and root gall formation varies among genotypes (Merz et al. 2012). Overall, the tuber and root phases of the disease were found significantly correlated, but the usefulness of this predictor was considered not suitable since cultivars showing tuber resistance can develop high rates of root galls (Hughes 1980). Two examples are the cultivars Umatilla Russet and Russet Burbank, which develop low levels of powdery scab on tubers, but are considered susceptible to root gall formation (de Boer 1991; Houser and Davidson 2010; Manzer et al. 1964; Merz et al. 2012).

The development of management approaches aimed to control the field expression of *S. subterranea* in the short and long-term are likely to be influenced by the degree of susceptibility on roots and tubers. Moreover, the genetic component of host resistance against formation of root galls was shown moderately high on potato genotypes evaluated in the Columbia Basin (Nitzan et al. 2010). In that study, 18 of 24 tested potato genotypes were genetically stable before and/or after removing the environmental heterogeneity. Therefore, host resistance represents the most advantageous and long-term approach for disease management; nevertheless, most reports are focused on powdery scab on tubers and to a lesser extent root gall formation (Baldwin et al. 2008; de Boer 1991; Falloon et al. 2003; Houser and Davidson 2010; Kirkham 1986; Nitzan et al. 2008; Torres et al. 1995; Wastie et al. 1988). The objective of this research was to determine if 113 potato genotypes with varying skin types differed in susceptibility to powdery scab and root gall formation.

Materials and Methods

Field Experiments

Experiments were conducted on irrigated commercial fields naturally infested with *Spongospora subterranea* and with a known history of disease. A total of five trials were performed during two consecutive years at four locations: Larimore, North Dakota (Larimore-11); McCanna, ND (McCanna-11; −12); Perham, Minnesota (Perham-11) and Osage, MN (Osage-12; Table 1). Plant material consisted of 113 potato cultivars and advanced clones which included red-, russet-, white- and yellow-skinned genotypes from the North Dakota State University potato breeding program and the potato breeding program of the Instituto de Investigaciones Agropecuarias (INIA) of Chile (Table 2).

Field trials were conducted using a randomized complete block design with three replicates. Treatment plots consisted of 5-plant rows in both years of research. Seed pieces (60 to 100 g) were planted 0.3 m apart and 0.1 m depth; the distance between rows was 0.9 m. Weather conditions during the course of field trials (June 1 - October 31) were estimated from records of the two nearest weather stations to the site of the trials (Table 3). At McCanna trials, irrigation was 95.3 and 518.2 mm during 2011 and 2012, respectively. At Perham in 2011, the amount of irrigation totaled 175.3 mm, and 271.78 mm at Osage during 2012.

The amount of nitrogen applied at McCanna was 110 $kg \cdot ha^{-1}$ in 2011 and 319 $kg \cdot ha^{-1}$ in 2012. Applied nitrogen at Minnesota trials was 164.5 $kg \cdot ha^{-1}$ at Perham-11 and 339.3 $kg \cdot ha^{-1}$ in Osage-12. At McCanna, herbicide applications were conducted each year using pendimethalin (2.8 $l \cdot ha^{-1}$) and rimsulfuron (105 $g \cdot ha^{-1}$). Pest management was performed using the insecticides thiamethoxam, imidacloprid, abamectin and esfenvalerate at manufacturer recommended rates. The control of foliar disease (early and late blight) was done using chlorothalonil, fluopyram/pyrimethanil, boscalid and azoxystrobin at recommended rates for irrigated commercial potato crops in the Upper Great Plains of the USA.

Sampling and Disease Assessment

Powdery Scab

At harvest, all tubers over 40 g were collected, and stored for approximately 6 weeks at 12 °C, and evaluated for disease. Prior to disease evaluations, tubers were washed and dried overnight at room temperature. The presence of sporosori under microscope was used to distinguish *Spongospora subterranea* from lesions caused by other pathogens such as

Table 1 Environments, soil texture and pH, and number of potato genotypes by skin type evaluated under field condition for susceptibility to powdery scab on tubers and root gall formation

Environment					Skin type				Total genotypes per location
Year	Location	Soil texture	Soil pH	Planting / harvest date	Red	Russet	White	Yellow	
2011	Larimore, ND	Sandy loam	6.7	May 17 / September 27	n.t	31	2	n.t	33
	McCanna, ND	Sandy loam	5.6	June 18 / October 3	29	20	26	13	88
	Perham, MN	Sandy	7.4	May 9 / September 14	28	11	25	13	77
2012	McCanna. ND	Sandy loam	5.6	April 27 / September 7	25	31	21	7	84
	Osage, MN	Sandy loam	6.1	May 3 / September 4	23	31	21	5	80
	Total genotypes per skin type				34	35	30	14	

n.t. not tested

Table 2 Potato cultivars and advanced clones evaluated under field conditions for their susceptibility to powdery scab and root gall formation caused by *Spongospora subterranea*

Potato cultivar or advanced clone	Skin type	Environments tested	Powdery scab index	Root gall formation index	Potato cultivar or advanced clone	Skin type	Environments tested	Powdery scab index	Root gall formation index
AND00272-1R	Red	4	0.240	0.018	ND050082Cb-2Russ	Russet	4	0.015	0.005
ATND98459-1RY	Red	4	0.451	0.221	ND050105C-1Russ	Russet	4	0.036	0.012
Colorado Rose	Red	2	0.101	0.041	ND059769Ab-1Russ	Russet	2	0.029	n/a
Dakota Jewel	Red	4	0.039	0.051	ND060735-3Russ	Russet	3	0.017	0.019
Dakota Rose	Red	1	0.019	n/a	ND060742C-1Russ	Russet	4	0.084	0.035
Dakota Ruby	Red	4	0.201	0.115	ND060761B-3Russ	Russet	3	0.013	0.046
Dark Red Norland	Red	4	0.033	0.033	ND060766b-4Russ	Russet	4	0.000	0.039
Karu[a]	Red	4	0.012	0.012	ND060770B-5Russ	Russet	3	0.044	0.089
ND028842b-1RY	Red	2	0.114	n/a	ND060796AB-1Russ	Russet	4	0.024	0.085
ND050167C-3R	Red	2	0.130	n/a	ND070927-2Russ	Russet	3	0.041	0.036
ND060728-5R	Red	4	0.165	0.061	ND6400C-1Russ	Russet	4	0.301	0.169
ND060733b-4RY	Red	2	0.008	n/a	ND8068-5Russ	Russet	5	0.024	0.081
ND4659-5R	Red	4	0.108	0.060	ND8413-7Russ	Russet	5	0.026	0.059
ND8058-11R	Red	1	0.011	n/a	Ranger Russet	Russet	5	0.012	0.022
ND8314-1R	Red	4	0.132	0.144	Russet Burbank	Russet	5	0.001	0.169
Patagonia[a]	Red	2	0.004	n/a	Russet Norkotah	Russet	5	0.002	0.008
R90070-8[a]	Red	4	0.018	0.086	Umatilla Russet	Russet	5	0.009	0.233
R90096-5[a]	Red	1	0.075	0.101	Atlantic	White	2	0.023	0.031
R90160-5[a]	Red	2	0.533	n/a	CO 95051-7 W	White	2	0.010	n/a
R91129-11[a]	Red	4	0.023	0.055	Dakota Crisp	White	2	0.124	0.059
R90134-6[a]	Red	2	0.040	n/a	Dakota Pearl	White	2	0.367	0.174
R90213-6[a]	Red	2	0.009	n/a	Ivory Crisp	White	4	0.366	0.257
RA 20-6[a]	Red	4	0.013	0.062	Kennebec	White	4	0.644	0.567
RA 89044-45[a]	Red	4	0.236	0.258	Lamoka	White	4	0.153	0.438
RA 90213-60[a]	Red	3	0.128	n/a	MSL-292A	White	2	0.445	n/a
RC 72-35[a]	Red	4	0.048	0.036	ND060601CAB-2	White	2	0.020	n/a
RC 89-25[a]	Red	2	0.071	0.078	ND060715B-15	White	2	0.032	n/a
Red LaSoda	Red	4	0.613	0.153	ND060835C-4	White	4	0.122	0.025
Red Norland	Red	4	0.137	0.071	ND060847CB-1	White	2	0.107	n/a
Red Pontiac	Red	4	0.171	0.328	ND6956b-13	White	4	0.536	0.255
RG 47-3[a]	Red	2	0.137	0.029	ND7519-1	White	4	0.421	0.048
SPA 161[a]	Red	4	0.002	0.083	ND7550C-1	White	4	0.083	0.011
T10-12[a]	Red	3	0.301	n/a	ND8304-2	White	4	0.058	n/a
Viking	Red	4	0.236	0.140	ND8305-1	White	2	0.076	0.202
Alpine Russet	Russet	5	0.003	0.070	ND8307C-3	White	4	0.338	0.080
Alturas	Russet	2	0.004	0.031	ND8331Cb-2	White	4	0.251	0.091
AND00618-1RussY	Russet	3	0.052	0.016	ND8331Cb-3	White	4	0.076	0.017
AND01804-3Russ	Russet	4	0.000	0.151	ND8559-20	White	4	0.013	0.084
AND95279-5Russ	Russet	1	0.000	n/a	Nicolet	White	4	0.136	0.457
AND97279-5Russ	Russet	2	0.000	0.040	NY-138	White	2	0.004	n/a
AND99362-1Russ	Russet	1	0.000	n/a	NY-139	White	2	0.157	n/a
AND99362B-1Russ	Russet	2	0.000	0.007	R65A-70[a]	White	2	0.204	n/a
AOND95292-3Russ	Russet	3	0.003	0.072	RA 151-24[a]	White	4	0.006	0.155
Bannock Russet	Russet	5	0.014	0.033	Shepody	White	5	0.468	0.289
Dakota Russet	Russet	5	0.000	0.002	Snowden	White	4	0.021	0.254
Dakota Trailblazer	Russet	5	0.002	0.014	W2717-5	White	2	0.024	n/a
ND039194-1Russ	Russet	1	0.215	n/a	Puren[a]	Yellow	2	0.040	n/a
ND039194AB-1Russ	Russet	2	0.000	0.195	R87009-28[a]	Yellow	3	0.081	n/a
ND049289-1Russ	Russet	4	0.004	0.000	R89045-35[a]	Yellow	2	0.131	n/a
ND049381C-2Russ	Russet	3	0.102	0.035	R-91007-5[a]	Yellow	4	0.101	0.065
ND049423b-1Russ	Russet	4	0.014	0.010	RA 148-48[a]	Yellow	2	0.074	n/a
ND049517B-1Russ	Russet	3	0.027	0.024	RA 16-5[a]	Yellow	2	0.059	n/a
ND049546b-10Russ	Russet	5	0.017	0.013	RA 362-54[a]	Yellow	2	0.032	n/a
RA 517-123[a]	Yellow	4	0.040	0.041	RK 24-48[a]	Yellow	2	0.121	0.690
RA 519-50[a]	Yellow	2	0.072	n/a	Yagana[a]	Yellow	3	0.049	0.168
RA 82-4[a]	Yellow	2	0.000	n/a	Yukon Gold	Yellow	4	0.059	0.042
RC 60-109[a]	Yellow	4	0.019	0.112					

n/a not applicable

[a] genotype developed by the potato breeding program of the Instituto de Investigaciones Agropecuarias (INIA) of Chile

Table 3 Average air temperature and total precipitation at two weather stations in Minnesota and North Dakota at experimental locations in 2011 and 2012

State	Station	2011		2012	
		Air temperature (°C)	Precipitation (mm)	Air temperature (°C)	Precipitation (mm)
Minnesota	Alexandria	17.5	481.6	17.4	229.1
	Fergus	18.4	327.9	17.8	199.1
North Dakota	Grand Forks	17.3	316.2	16.4	256.0
	Inkster	16.6	338.8	16.2	273.2

Streptomyces spp. (Waterer 2010). Disease incidence was expressed as the percentage of infected tubers in a sample, and disease severity as the percentage of tuber surface covered by powdery scab lesions. Severity was estimated on each side of the tuber using an increasing percentage graphic scale and then averaged (Falloon et al. 1995). The mean disease severity was calculated as $\left[\sum \frac{(nN_n)}{5N_0}\right]$*100, where n is the disease index (0 = no disease, 1 = one pustule to 2.0 %, 2 = 2.1–5.0 %, 3 = 5.1–10.0 %, 4 = 10.1–25 %, 5 => 25 %) (Houser and Davidson 2010; Nakayama et al. 2007), N_n is the number of tubers with disease symptoms at level "n" and N_0 is the total number of tubers evaluated.

Root Gall Formation

Ninety days after planting, root galls were evaluated by carefully removing an entire plant from the soil with the aid of a potato fork. Root gall formation was only evaluated during the second year of research (McCanna-12 and Osage-12). Five plants per plot were sampled and the number of galls per plant was counted with the aid of a magnifying glass (1.75×). The mean number of galls per plant was calculated for each plot. The mean maximum number of galls per plant and powdery scab severity was also calculated for each location (Baldwin et al. 2008).

Statistical Analysis

Statistical analysis was conducted using SAS 9.3 (SAS Institute, Cary, NC). Homogeneity of variances was assessed during data analysis using Bartlett's test ($\alpha = 0.05$). Normal distribution of the data was evaluated using the Shapiro-Wilk test ($\alpha = 0.05$). Among genotypes, differences in the intensity of root gall formation and powdery scab parameters were estimated using Friedman's test on ranked data. The effect of location and year on the development of powdery scab incidence and severity was assessed on a set of 15 potato cultivars across four trials. Data on powdery scab parameters were square root transformed ($\sqrt{y}$) and analyzed by ANOVA as randomized complete block design with potato cultivar as a sub-sample. Treatment means were compared using Fisher's protected least significant difference (LSD; α: 0.05).

Spearman's rank correlation was performed in order to assess the degree of association between powdery scab incidence and severity on a sub-set of 50 potato genotypes. On this data set, the broad-sense heritability (H) for powdery scab incidence and severity on tubers were calculated for trials conducted in North Dakota and Minnesota. H as the proportion of the phenotypic variation given by the genotypic variance was defined as $H = \sigma^2_G / [(\sigma^2_{error} / re) + (\sigma^2_{GxE} / e) + \sigma^2_G)]$, where r = number of replicates and e = number of environments (Holland et al. 2003). The 95 % confidence intervals for H were determined according to Knapp et al. (1985). The upper confidence interval was 1-[(MS1/MS2) $F_{(1-\alpha/2:df2,\ df1)}]^{-1}$, and the lower confidence interval 1-[(MS1/MS2) $F_{(\alpha/2:df2,\ df1)}]^{-1}$, where MS1 = mean squares for genotype and MS2 = mean squares for genotype x environment. The mean squares associated with the random effects were obtained from ANOVA analysis.

Data for powdery scab severity and root gall formation of 80 potato genotypes evaluated in at least two environments were standardized by dividing the averaged disease severity and mean number of galls by the mean maximum value of each variable at a specific environment (Y/Y_{max}). This procedure was chosen in order to adjust for major environmental differences in disease expression across trials (Falloon et al. 2003). The powdery scab and root gall formation indices of the genotypes included in this sub-set were averaged across environments, plotted and subjected to cluster analysis using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). Potato genotypes were categorized according to arbitrary cut-off points as very resistant (VR: 0 to 0.05), moderately resistant (MR: > 0.05 to 0.15), moderately susceptible (MS: > 0.15 to 0.25) and very susceptible (VS: > 0.25). Cut-off points for susceptibility ranks were adjusted according to cluster groupings. The significance among genotype rankings for each disease phase was verified using multiple t-tests. Differences in powdery scab and root gall formation indices among skin types were tested using the Median Test. The relationship between powdery scab and root gall formation indices and the susceptibility rank of genotypes across environments were evaluated using Spearman's rank correlations.

Results

Susceptibility of Potato Genotypes to Powdery Scab and Root Gall Formation

Powdery scab and root gall formation developed at all trial locations. Differences in disease expression among genotypes were significant in most of the trials; no differences were observed for powdery scab on genotypes planted at Larimore-11 and root gall formation at Osage-12. During the first year of evaluation, mean powdery scab incidence ranged from zero to 11.4 % at Perham-11. In this trial, the highest incidences were detected on the cultivars Ivory Crisp (11.4 %) and Shepody (11 %) and the advanced clone ND7519-1 (11.2 %). In McCanna-11, disease incidence ranged from zero to 73.9 %. Advanced clones ND6956b-13 (73.9 %) and ND8307C-3 (48.2 %) and cultivar Kennebec (50.8 %) had the highest mean incidences. At Perham-11, the highest mean severities were observed on cultivars Red LaSoda (2.8 %) and Kennebec (2.7 %) and the advanced clone ND7519-1 (3.0 %) whereas at McCanna-11, the highest mean severities were observed on clones ND6956b-13 (23.3 %), ND8307C-3 (20.7 %) and T10-12 (16.6 %). The cultivar Red LaSoda (2.9 %) and the clone AND00272-1R (11.2 %) had the highest mean maximum severities at Perham-11 and McCanna-11, respectively. Genotypes showing no powdery scab symptoms included the clones T10-12, R65A-70, R90213-6 at Perham-11, and RA 82-4, SPA 161, R65A-70 at McCanna-11.

In 2012, mean powdery scab incidence ranged from zero to 18.1 % at Osage-12 and from zero to 52.8 % in McCanna-12. The advanced clones ND6956b-13 (18.1 %), ND7519-1 (10.2 %), ND8331Cb-2 (5.6 %) showed the highest incidences at Osage-12, while at McCanna-12 the highest incidences were observed on the cultivars Kennebec (52.8 %), Red LaSoda (52.4 %) and Dakota Pearl (50.7 %). These cultivars also had the highest mean severities with 29, 26.2 and 19.4 %, respectively. At Osage-12, the highest mean severities were observed on the cultivar Shepody (1.4 %) and the advanced clones ND6956b-13 (5.9 %) and ND7519-1 (2.4 %). The clone ND6956b-13 (2.4 %) at Osage-12, and the cultivar Kennebec (40 %) at McCanna-12, had the highest mean maximum severities.

No powdery scab symptoms were observed on genotypes AND01804-3Russ, R91129-11, RC89-25, ‘Karu’, SPA161 and RA151-24 grown at Osage-12 and McCanna-12. However, root galls developed in all genotypes tested at McCanna-12. In this trial, the highest number of galls per plant were observed on the cultivars Lamoka (149.6 galls), Kennebec (115.3 galls) and Red Pontiac (77.8 galls). Conversely, the cultivar Dakota Russet (0.6 galls) and the advanced clones T10-12 (0.5 galls) and ND049289-1Russ (‘MonDak Gold’ × ‘Dakota Trailblazer’; < 0.1 galls) had the lowest number of galls per plant.

Based on disease indices across field trials, no powdery scab was observed on tubers of nine potato genotypes tested in at least two environments (Table 2). Among asymptomatic genotypes, most were russet-skinned (e.g. AND97279-5Russ, AND99362B-1Russ, ‘Dakota Russet’ and ND039194AB-1Russ) but also included a yellow-skinned clone (RA 82-4; Table 2). Although the absence of root galls under conditions of high disease pressure was not observed, the advanced clone ND049289-1Russ had the lowest amount of root galls per plant across trials. This genotype yielded only one root gall in 30 plants tested at two environments.

Powdery Scab Across Environments

Across locations, significant differences were observed between mean powdery scab incidence and severity developed in trials conducted in North Dakota and Minnesota ($P < 0.001$, $n = 90$) in 2011 and 2012. However, no differences were observed for mean powdery scab incidence ($P = 0.394$, $n = 90$) and severity ($P = 0.671$, $n = 90$) in trials conducted in North Dakota or Minnesota during two consecutive years (Fig. 1). At McCanna-11 the

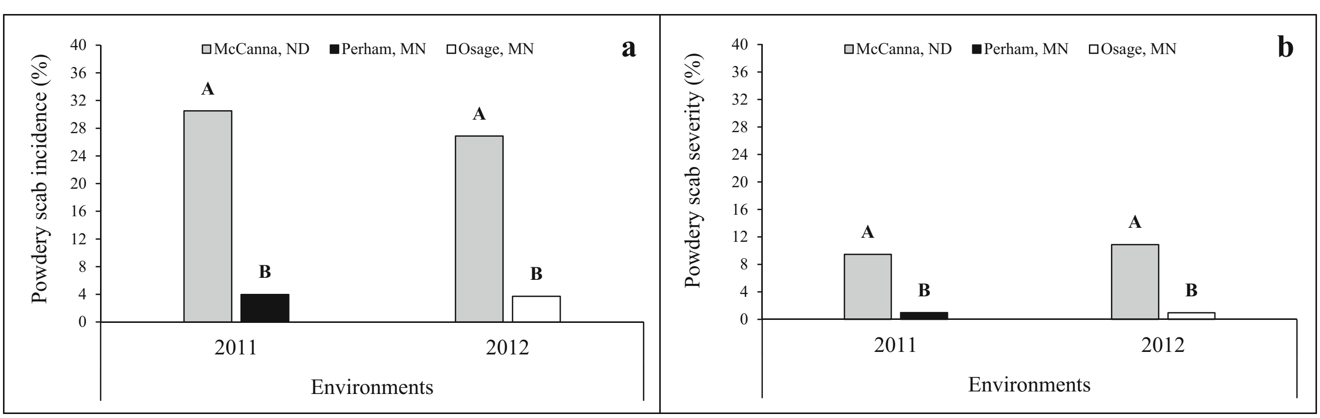

Fig. 1 Mean powdery scab incidence (**a**) and severity (**b**) across evaluated environments in Minnesota and North Dakota during 2011 and 2012. Means of 45 five-plant plots. Means across environments with different letter are different (LDS$\alpha = 0.05$). Non-transformed data are presented

mean powdery scab incidence and severity on selected genotypes were 30.5 and 9.5 % respectively. At McCanna-12, a similar mean disease incidence (26.9 %) and severity (10.9 %) was observed. The mean disease incidence and severity found at Perham-11 was 3.7 and 1 % respectively, whereas at Osage during 2012, powdery scab incidence was 3.7 % and disease severity was 0.9 %. Overall disease incidence and severity were about seven and 10 times higher in North Dakota than the Minnesota environments.

Broad-Sense Heritability and the Relationship of Powdery Scab Incidence and Severity

The broad-sense heritability (H) for powdery scab severity was calculated on a set of 50 potato genotypes from four environments in Minnesota and North Dakota (McCanna-11 and 12, Perham-11 and Osage-12); estimates were obtained separately for environments and combination of environments. For trials preformed in ND, H for powdery scab incidence was 0.76, and 0.63 for disease severity. The 95 % confidence intervals (C. I.) for powdery scab incidence and severity were 0.57 to 0.86 and 0.35 to 0.79, respectively. In Minnesota environments, estimates of H were 0.45 for disease incidence (C. I.: 0.03 to 0.69) and 0.40 for disease severity (C. I.: 0 to 0.66). Across all environments, the broad-sense heritability for disease incidence was 0.66 (C. I.: 0.47 to 0.78) and 0.55 for disease severity (C. I.: 0.31 to 0.71).

Powdery scab mean severity was strongly associated to disease mean incidence ($P < 0.001$, $n = 50$) at each tested environment. In North Dakota (McCanna), Spearman's correlation coefficient (r) was 0.99 during 2011 and 2012, and in Minnesota, r was 0.99 for both Perham in 2011 and Osage during 2012.

Susceptibility Ranking and Association of Disease Phases

Powdery scab and root gall formation indices were calculated for 80 potato genotypes tested in at least two trials. Among genotypes, the indices for the tuber phase of the disease ranged from zero to a high of 0.644 for the cultivar Kennebec. At the same time, low disease indices were observed on smooth-skinned cultivars such as Dark Red Norland (0.033) and Snowden (0.021) (Table 3). Root gall formation indices ranged from <0.001 for the advanced clone ND049289-1Russ to 0.69 on RK 24-48. Low root gall formation indices were also observed on cultivars such as Dakota Russet (0.002), Russet Norkotah (0.008) and Karu (0.012). Overall, root and tuber indices were more widespread on red and white-skinned genotypes compared to russet and yellow-skinned genotypes.

Among tuber skin types, most genotypes showing low disease indices (<0.05) for either the root and tuber phase of the disease were russet- and yellow-skinned; however, low disease indices were also observed among some red- and white-skinned genotypes. Overall, the highest powdery scab indices were observed on red- (0.613) and white-skinned genotypes (0.644; Table 2), whereas the highest root gall formation indices were observed on yellow- (0.69) and white-skinned (0.567) genotypes. Calculated indices for the root and tuber phase of the disease in russet-skinned genotypes were significantly lower than those from smooth-skinned genotypes ($P < 0.05$, $n = 80$; Fig. 2).

The degree of association between powdery scab and root gall formation indices of 80 potato genotypes across locations and skin types was observed significantly associated ($r = 0.42$; $P < 0.001$). Similar results were noted for the degree of association between disease on roots and tubers of red- ($r = 0.48$; $P = 0.021$; $n = 23$) and white-skinned genotypes ($r = 0.52$; $P = 0.019$; $n = 20$). In contrast, this association was absent on russet- ($r = -0.03$; $P = 0.86$; $n = 31$) and yellow-skinned

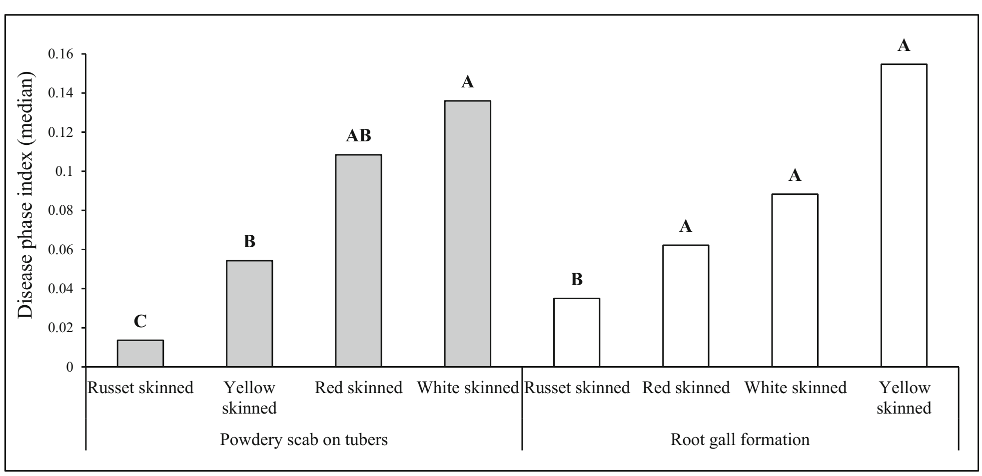

Fig. 2 Powdery scab and root gall formation index medians of potato genotypes of four skin types (market class) planted in field trials conducted in Minnesota and North Dakota. Treatment medians with different letter are significantly different according to median test ($\alpha = 0.05$)

genotypes (r = 0.37; $P = 0.42$; $n = 6$). However, a significant association was observed for russet-skinned genotypes when data was combined with either red- (r = 0.27; $P = 0.045$; $n = 54$) or white-genotypes (r = 0.40; $P = 0.004$; $n = 51$). In addition, a significant association between disease on tubers and roots was recorded when data for yellow-skinned genotypes was combined with either red- (r = 0.40; $P = 0.034$; $n = 29$) or white-genotypes (r = 0.45; $P = 0.022$; $n = 26$), but absent when combined with russet-skinned genotypes data (r = 0.16; $P = 0.357$; $n = 37$). Although a significant association between powdery scab and root gall formation was observed overall, for some skin-types and for most skin-types combinations, the highest degree of association was 0.52.

Potato genotypes were ranked according to their susceptibility to powdery scab and root gall formation using arbitrary cut-offs points (Table 4). Genotypes ranked as very resistant to root gall formation included red-, white-, russet-, and yellow-skinned cultivars and advanced clones with indices ranging from <0.001 to 0.006. Genotypes ranked as very susceptible to Spongospora root gall formation comprised red-, white-, and yellow-skinned cultivars and advanced clones. Root gall formation indices among these genotypes ranged from 0.254 to 0.690. Conversely, among russet-skinned genotypes the highest root gall formation index was observed on cultivar Umatilla Russet (0.233). Powdery scab indices for potato genotypes ranked as very resistant ranged from zero to 0.076. Alternatively, powdery scab indices for genotypes ranked as very susceptible ranged from 0.301 to 0.644; most of these genotypes were red- and white-skinned. Potato genotypes ranked as very resistant to powdery scab and root gall formation accounted for 32.5 % of those evaluated. Within this rank, most of the genotypes were russet-skinned (73.1 %), but some white- ('Atlantic'), red- ('Dakota Jewel', 'Dark Red Norland', 'Karu' and RC 72-35) and yellow-skinned (RA 517-123 and 'Yukon Gold') yielded a similar response. On the other hand, only 6.25 % of the evaluated genotypes ranked as very susceptible to powdery scab and root gall formation. Potato cultivars Snowden, Russet Burbank and Umatilla Russet were ranked as resistant to tuber powdery scab but were susceptible to root gall formation. Furthermore, susceptibility indices for powdery scab were observed highly associated ($P < 0.001$, $n = 80$) among environments, with r values ranging from 0.48 to 0.76 (Table 5).

Based on skin type, the proportion of genotypes with resistance to powdery scab was significantly higher than the proportion of genotypes susceptible to this phase of the disease ($P = 0.002$, $n = 80$; Fig. 3). Similar results were observed for the development of root galls ($P = 0.033$, $n = 80$; Fig. 3). In

Table 4 Potato genotype rankings according to their susceptibility level to powdery scab on tubers and root gall formation caused by *Spongospora subterranea*

		Root phase[a]				
		Very resistant		Moderately resistant	Moderately susceptible	Very susceptible
Tuber phase[a]	Very resistant	Alturas AND00618-1RussY AND97279-5Russ AND99362B-1Russ Atlantic Bannock Russet Dakota Jewel Dakota Russet Dakota Trailblazer Dark Red Norland Karu ND049289-1Russ ND049423b-1Russ	ND049517B-1Russ ND049546b-10Russ ND050082Cb-2Russ ND050105C-1Russ ND060735-3Russ ND060761B-3Russ ND060766b-4Russ ND070927-2Russ RA 517-123 Ranger Russet RC 72-35 Russet Norkotah Yukon Gold	Alpine Russet AOND95292-3Russ ND060770B-5Russ ND060796AB-1RUss ND8068-5 ND8413-7Russ ND8559-20 R 90070-8 R 91127-11 RA 20-6 RC 06-109 RC 89-25 SPA 161	AND01804-3Russ ND039194AB-1Russ ND8305-1 RA 151-24 Russet Burbank Umatilla Russet Yagana	Snowden
	Moderately resistant	Colorado Rose ND049381C-2Russ ND060742C-1Russ ND060835C-4	ND7550C-1 ND8331Cb-3 R 90096-5 RG 47-3	Dakota Crisp ND4659-5R R 91007-5 Red Norland	ND8314-1R	Lamoka Nicolet RK 24-48
	Moderately susceptible	ND060728-5R AND00272-1R		Dakota Ruby ND8331Cb-2 Viking		RA 89044-45 Red Pontiac
	Very susceptible			ND7519-1 ND8307C-3	ATND98459-1RY Dakota Pearl ND6400C-1Russ Red LaSoda	Ivory Crisp Kennebec ND6956b-13 Shepody

[a] Potato genotypes ($n = 80$) evaluated in at least two environments were ranked into four categories according to their root and tuber phase indices using arbitrary cut-off points: very resistant (0 to 0.05), moderately resistant (> 0.05 to 0.15), moderately susceptible (> 0.15 to 0.25) and very susceptible (> 0.25)

Table 5 Relationship among potato genotypes susceptibility indices for powdery scab on tuber across environments evaluated in Minnesota and North Dakota during 2011 and 2012

Compared environments		McCanna-11	McCanna-12	Osage-12
McCanna-12	r	0.76		
	P-value	<0.001		
Osage-12	r	0.64	0.52	
	P-value	<0.001	<0.001	
Perham-11	r	0.51	0.57	0.48
	P-value	<0.001	<0.001	<0.001

r Spearman's rank correlation coefficient

contrast, no differences were observed between the proportion of potato cultivars and advanced clones with resistance to powdery scab on tubers. Potato cultivars with resistance to powdery scab accounted for 75 %, whereas the proportion of resistant advanced clones was about 81 %. However, these proportions differed significantly for root gall formation ($P = 0.046$, $n = 80$) for which, advanced clones with resistance to root symptoms accounted for near 81 % compared to the proportion of resistant cultivars which was about 57 %.

Discussion

The degree of susceptibility to disease caused by *S. subterranea* on tubers and roots of 30 potato cultivars and 83 advanced clones were tested and differences were observed. Although most of the resistant genotypes were russet-skinned, some of the smooth-skinned genotypes (e. g. 'Atlantic', 'Karu', 'Snowden', 'Yagana' and 'Yukon Gold') showed good levels of resistance against powdery scab. However, potato cultivars resistant to powdery scab but susceptible to root gall formation were also noted (e. g. 'Umatilla Russet', 'Russet Burbank' and 'Snowden'). Potato cultivars such as Kennebec and Shepody were very susceptible to powdery scab in agreement with previous reports (Christ and Weidner 1988; Falloon et al. 2003; Kirkham 1986). Overall, the degree of association between the two phases of the disease was significant, but the usefulness of the formation of galls as a predictor of powdery scab remains unsuitable, as large amounts of root galls developed in potato genotypes in which low amount of powdery scab symptoms were observed. In addition, results described here suggests that susceptibility to root gall formation follows a continuum from very susceptible to very resistant.

Disease pressure across environments differed between Minnesota and North Dakota locations. On average, severity of powdery scab at McCanna, ND, was 10.3 times higher than in Minnesota. Powdery scab and root gall formation are favored by cool soil temperatures (12 to 17 °C) and abundant soil moisture (de Boer et al. 1985; van de Graaf et al. 2005, 2007); these conducive conditions appear to be more important around mid-season, coinciding with early tuber formation (Diriwächter and Parbery 1991; Taylor et al. 1986). Furthermore, powdery scab incidence and severity of field experiments kept at field capacity, differed significantly between planting dates in June (Christ and Weidner 1988). In those experiments, soil temperature was higher at late planting (mid-June) resulting in lower disease expression. During the first year of this research, average air temperatures at

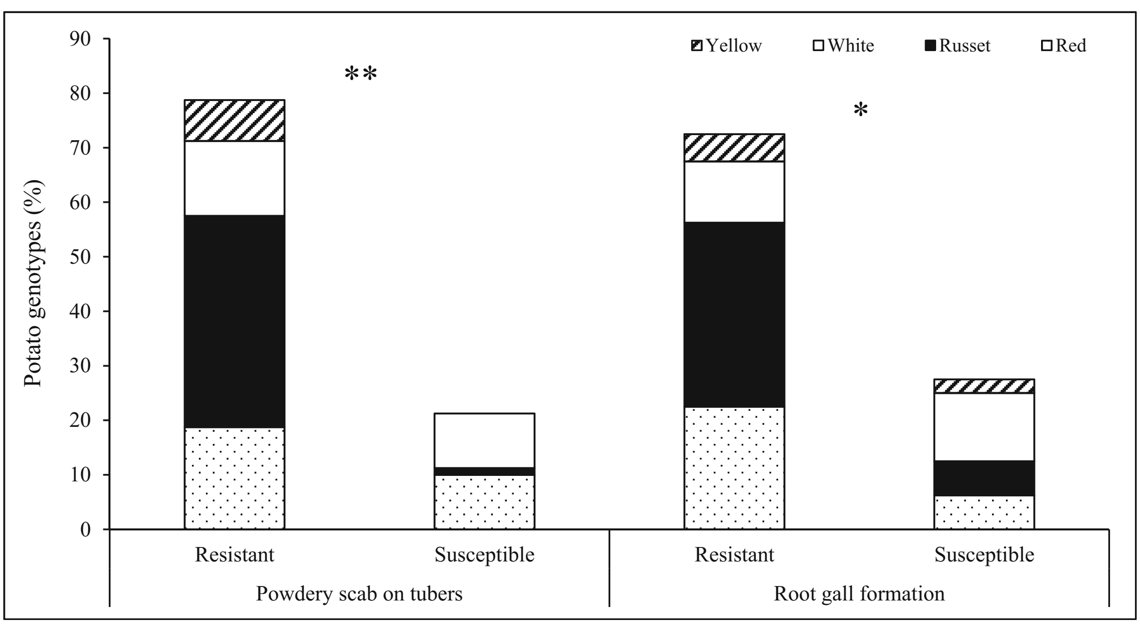

Fig. 3 Proportion of potato genotypes of four skin types (market class) ranked as resistant or susceptible to powdery scab on tubers and root gall formation. $n = 80$. *: $P < 0.05$. **: $P < 0.01$

Minnesota locations were 17.5 °C in Alexandria and 18.4 °C in Fergus Falls, and in North Dakota, 17.3 °C and 16.7 °C at Grand Forks and Inkster, respectively. During 2012, average air temperatures in Minnesota were 17.4 °C at Alexandria and 17.8 °C at Fergus Falls, whereas in North Dakota, temperatures were 16.4 °C in Grand Forks and 16.2 °C at Inkster. It is likely that temperature had influenced differences in disease development observed between North Dakota and Minnesota.

Despite environmental conditions, powdery scab and root gall formation developed in all trials at all locations. In this sense, severity of powdery scab varied substantially across experiments on selected susceptible cultivars such as Kennebec (0.6 to 29 %). On resistant cultivars, severity on tubers ranged from 0 to 4.1 %, and on russet-skinned cultivars from 0 to 0.3 %. However, although disease pressure differed substantially among site years due to environmental conditions, susceptibility ranking of genotypes based on powdery scab indices were significantly associated among locations and years, indicating a similar response of genotypes against disease caused by *S. subterranea*. In potato, resistance to powdery scab is based on multiple genes which have been suggested to act as buffers against environmental stresses (Falloon et al. 2003; Merz et al. 2012). Under European conditions, no evidence of a genotype x environment interaction due to pathogen genetic diversity was observed (Merz et al. 2012). At the same time, the variability of European *S. subterranea* isolates was found lower compared to South American populations included in a global study of the diversity of the pathogen (Gau et al. 2013). In that research, the lowest variability among countries was observed in the North American populations. In addition, differences based on genetic variability of the pathogen were observed among, but not within, locations of the US (Qu and Christ 2006). In this research, the overall degree of diversity was relatively low, however, *S. subterranea* isolates from California, Idaho, North Dakota and Washington grouped differently than those from Colorado, Maine and Pennsylvania (Qu and Christ 2006).

Under conditions of low pathogen diversity, host resistance represents a viable alternative for disease management, which at the same time may benefit by the presence of multiple genes of resistance on the host (Falloon et al. 2003; Gau et al. 2013). Additionally, the genetic mechanisms controlling *S. subterranea* infection and spread in roots appears to be different than those involved in the expression of symptoms in roots and tubers (Hernandez Maldonado et al. 2013). Estimates of broad-sense heritability (H) suggest that resistance to root gall formation as a trait can be easily deployed into genotypes under development (Nitzan et al. 2010). Our estimations of H at locations under high disease pressure (i.e. North Dakota) suggest a moderately high genetic component for powdery scab incidence and severity, as values for H were calculated as 0.76 and 0.63, respectively. However, this aspect of disease resistance requires additional research to further substantiate this H value.

Spongospora subterranea is able to infect and cause disease on the cultivated potato (*S. tuberosum* ssp. *tuberosum*, spp. *andigena* and *S. phureja*). Furthermore, *S. subterranea* is the vector of the *Potato mop-top virus*, a pathogen of growing concern, as reports show an increase in distribution (David et al. 2010; Crosslin 2011; Lambert et al. 2003; Mallik and Gudmestad 2015; Whitworth and Crosslin 2013). Despite the effect the pathogen on potato and its importance as vector of PMTV, the amount of research focused on identifying sources of resistance among *Solanum* species is scarce. Resistance to root infection was observed in *S. acaule* among other tested species including *S. sucrense* and *S. brevides* (Mäkäräinen et al. 1994). Other sources of resistance include clones of the species *S. phureja* (Lahuf et al. 2014; Lees 2000), which has the peculiarity of developing only root galls, suggesting specific resistance to tuber infection (Gau et al. 2013). Among potato selections showing resistance to root gall formation in the Columbia Basin (WA), two common characteristics were observed: resistant genotypes derived from the introgression of *S. bulbocastanum*, and at the same time, the cultivar Summit Russet appearing more than once in their background (Nitzan et al. 2008). In our study, some of the potato genotypes ranking as very resistant to both phases of the disease were found to have the cultivar Summit Russet appearing in their pedigree (ND049289-1Russ and 'Dakota Trailblazer'). The cultivar Dakota Russet which also ranked as very resistant is an example of the introgression of *S. raphanifolium* along with other resistant cultivars such as Atlantic. Other examples of the introgression of wild species into cultivars with resistance to powdery scab and root gall formation are 'Yukon Gold' which has *S. phureja* and *S. acaule* in its background, and 'Atlantic' with *S. chacoense* (Plaisted and Hoopes 1989).

Potato production in Minnesota and North Dakota accounts for about 10 % of the US market (USDA 2014b). In addition, North Dakota is ranked as the second largest certified seed producer in the US, in which around 33 % of the potato production in North Dakota is represented by smooth-skinned cultivars (USDA 2014b). Results presented in this study indicate the relative levels of susceptibility among potato genotypes and demonstrate the existence of resistance to powdery scab and root gall formation in potato genotypes originated in the North and South America. These results can assist potato breeders in the selection of genotypes for future development of potato cultivars with resistance to both phases of the disease. The management of powdery scab on tubers and root gall formation through cultivar selection is highly recommended. Further research will be required in order assist breeding and selection through molecular approaches that enable resistance detection of both phases of the disease across potato market classes.

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