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Genome-Wide Association Study of Resistance to Potato Common Scab

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Abstract

Potato common scab caused by bacterial pathogen *Streptomyces scabies* (Thaxt.) Waksman & Henrici is one of the most important diseases of potato (*Solanum tuberosum* L.) worldwide. Currently, the most effective and desirable method to control common scab is through the use of resistant cultivars. In order to decipher the genetic control of resistance to common scab disease in Canadian potato germplasm, an association panel of 143 clones including advanced breeding clones and commercial cultivars was genotyped with 12K SolCAP SNPs and phenotyped for potato common scab resistances in multiple years. By conducting a genome-wide association analysis (GWAS) using GWASpoly R package, three resistance QTLs were identified on potato chromosomes 2, 4, and 12, respectively. The phenotypic variation explained by these QTLs was 21%, 19%, and 26%, respectively. The QTL on chromosome 2 was simplex-dominant whereas duplex-dominant QTLs were identified on chromosomes 4 and 12. These findings will be useful to design marker-assisted selection and breeding strategies to improve resistance to common scab in new potato cultivars.

Keywords Common scab resistance · Genome-wide association study (GWAS) · QTL · SNPs

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Introduction

Potato common scab caused by soilborne gram-positive bacteria in the genus *Streptomyces* is one of the most commercially devastating potato diseases (Loria 2001; Hill and Lazarovits 2005; Hao et al. 2009). Among several hundred species of *Streptomyces*, *S. scabies* (Thaxter) Waksman & Henrici was one of the few species that is pathogenic on potato plants (Waksman and Henrici 1948; Lambert and Loria 1989; Braun et al. 2017a, b). Many more pathogenic *Streptomyces* including *S. turgidiscabies* and *S. acidiscabies* also cause scab diseases in potato worldwide (Miyajima et al. 1998; Kim et al. 1999; Kreuze et al. 1999; Lehtonen et al. 2004; St-Onge et al. 2008; Zhao et al. 2008; Thwaites et al. 2010; Dees et al. 2013). Potato common scab produces pitted corky lesions on the periderm of potato tubers which result in downgrading or rejection of affected tubers. The incidence and severity of common scab can vary depending on the distribution of the pathogen, environmental conditions, and host-pathogen interaction (Bukhalid et al. 1998; Hill and Lazarovits 2005; Lazarovits et al. 2007). Structural properties of potato skin and the sensitivity to the toxin, thaxtomin, produced by *S. scabies* are considered to be factors contributing to the cultivar susceptibility. The management of potato scab disease can be complicated by environmental factors including soil pH, moisture, and microbial components of the soil (Peters et al. 2004; Sturz et al. 2004; Weinert et al. 2011; Dees and Wanner 2012). Control measures often fail because little is known about the pathogenesis and contrasting requirements of favourable conditions for different diseases (Wang and Lazarovits 2005; Wilson et al. 2009).

Currently, the most effective and desirable method to combat the soilborne disease is to develop resistant cultivars. Potato resistance to common scab has been investigated in a number of studies (Goth et al. 1993; Murphy et al. 1995; Haynes et al. 2010). In most cases, the resistance appeared to be quantitatively inherited with continuous distribution (Driscoll et al. 2009; Haynes et al. 2010). Alam (1972) suggested that resistance was controlled by two independent loci. The resistance appears to require the presence of a single dominant allele at the first locus, and the presence of two homozygous recessive alleles at the second locus. This model was supported by Murphy et al. (1995), who successfully demonstrated the transmission of scab resistance from the diploid to the tetraploid background. However, unlike the simple genetic control of most loci in diploid populations, the inheritance of multiple alleles at a locus is complicated in commercial cultivars or tetraploid germplasm, due to tetrasomic segregation (Wricke and Weber 1986) and the resistance to common scab appears as a quantitatively inherited trait (Haynes et al. 2009). Furthermore, the allele dosage may affect the level of gene expression and result in different phenotypes (Guo et al. 1996).

Genome-wide association studies (GWAS) are a powerful tool to identify marker variants that are significantly associated with complex traits (Pritchard et al. 2000; Kang et al. 2008, 2010; Zhang et al. 2010). Unlike traditional mapping studies using biparental populations, GWAS usually use a germplasm panel taking the marker-estimated population structure and marker-estimated kinship as covariates (denoted Q and K, respectively). Rosyara et al. (2016) developed an R package, GWASpoly to conduct GWAS in autopolyploid populations using Q + K linear mixed model with bi-allelic SNPs. The detection power of the platform was also validated in a tetraploid

potato diversity panel, which was genotyped using 8303 SNPs as part of the USDA-NIFA Solanaceae Coordinated Agricultural Project (SolCAP) (Hamilton et al. 2011; Felcher et al. 2012; Hirsch et al. 2013). The objective of this study was to identify loci significantly associated with common scab disease resistance in a Canadian potato germplasm panel using the GWASpoly software.

Materials and Methods

Plant Material

The study was conducted at the Fredericton Research and Development Centre of Agriculture Agri-Food Canada (AAFC, Fredericton, New Brunswick). An association panel of 143 clones including 20 commercial cultivars and 123 advanced breeding clones was used in the analysis. The advanced breeding clones were mainly developed for the processing and fresh markets. They were chosen based on their breeding potential or agronomic merits following many years of field selection at the Benton Ridge Breeding substation of Agriculture Agri-Food Canada. Commercial cultivars in this panel represented a range of materials that are commercially grown in North America, and some were used as parental lines in the AAFC potato breeding program. Plant materials were planted in a scab nursery maintained at AAFC's Experimental Farm (Fredericton, New Brunswick, Canada). The field was repeatedly used to grow cultivated potato over past 10 years in order to promote high disease pressure of potato common scab (*Streptomyces scabies* (Thaxt.) Waksman & Henrici). The experiment was carried out using a randomized block design with three replications. Each block consisted of 16 rows, each 102.4 m long. Individual plots consisted of 10 hills planted in 4.3-m-long rows. In these field trials, every 4 rows were bordered by a check row of a susceptible variety, Green Mountain. Data used in the study were obtained from evaluations conducted in 2012, 2014, and 2016 at Fredericton. Tubers were rated at harvest for pustule type (1–5 scale) and surface area covered. Raw data were converted to a relative percentage of the susceptible check. The percentage values were then indexed on a 1–9 scale of increasing susceptibility. Usually, Green Mountain (susceptible check) has a score of 8, whereas Hindenburg (resistant check) has a score of 2 on this scale.

DNA Extraction and Genotyping

Potato genomic DNA was extracted from young leaf tissue following the standard CTAB (cetyltrimethyl ammonium bromide) method (Hoisington et al. 1994). The association panel was genotyped using the Illumina 12K SolCAP BeadChip (Illumina, San Diego, USA) by NeoGen Inc. (Lansing, MI, USA). The Theta values of samples were obtained using Illumina's GenomeStudio software (Illumina, San Diego, CA, v2011.1) following the company's protocol. The quality of each SNP was visually inspected using Excel sorting function. The SNPs without assigned physical positions on potato genome were mapped to physical position in genome using the BLAST tool in Spud DB (http://solanaceae.plantbiology.msu.

edu/integrated_searches.shtml). Non-polymorphic SNPs (minor allele frequency < 5%) were discarded from the dataset. R-script (fitTetra) was used to convert the Theta value from GenomeStudio into five types of potato genotypes, nulliplex (AAAA), simplex (AAAB), duplex (AABB), triplex (ABBB), and quadriplex (BBBB) states (Voorrips et al. 2011). These bi-allelic SNP genotypes in autotetraploids were then converted into the dosage of the minor alleles, 0, 1, 2, 3, and 4 for nulliplex, simplex, duplex, triplex, and quandriplex, respectively.

Statistical Analysis and Heritability

Neighbour-joining (NJ) trees were generated to visually decipher the population stratification by a pairwise distance matrix derived from the Nei's genetic distance for all polymorphic SNPs using PowerMarker version 3.25 (Liu and Muse 2005) and displayed on Figtree version 1.4.3 (Rambaut 2016). Both linear regression and analysis of variance (ANOVA) in R (www.r-project.org) were used to conduct the analysis of the phenotypic traits. A principal component analysis (PCA) was conducted for phenotypic traits used as selection criteria as a complementary approach to estimate population structure in the association panel (Joliffe 2002). The detailed definition of field selection traits and PCA were described in our previous study (Yuan et al. 2016). The broad-sense heritability (h^2) for common scab resistance was estimated on a phenotypic mean basis using R according to Wricke and Weber's algorithm (Wricke and Weber 1986).

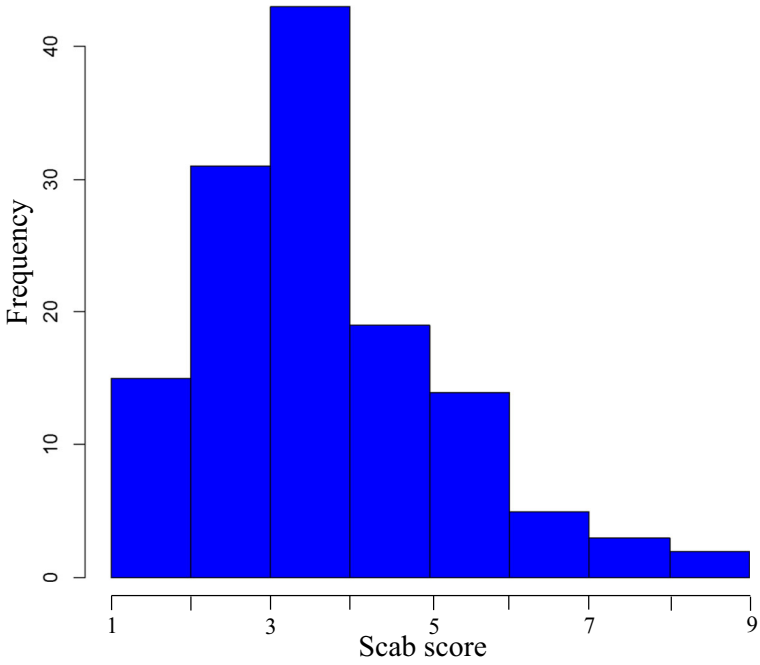

Fig. 1 Distribution of common scab ratings in the study panel. The disease was scored on a 1–9 scale where 1 is the disease free on the surface of tubers and 9 has the worst disease symptom on tubers. The estimated broad-sense heritability (h^2) for common scab resistance based on the field evaluation in 2012, 2014, and 2016 was 0.81

Genome-Wide Association Mapping

The R package GWASpoly for tetrapolyploids (Rosyara et al. 2016) was used to conduct the GWAS analysis on the panel. Principal component analysis was used to estimate the population stratification using prcomp algorithm (www.r-project.org). The top four principal components were used to build up the P matrix for population structure correction. Kinship matrices were calculated with the algorithm built in GWASpoly package. The Q + K linear mixed model under P3D was used to test the associations between the SNPs and phenotypic variations (Rosyara et al. 2016). In addition to the general model, four different genetic models (additive, simplex dominant, duplex dominant, and diploidized additive) were tested. In the additive models, the SNP effect is proportional to allele dosage. For dominant models, tests were done

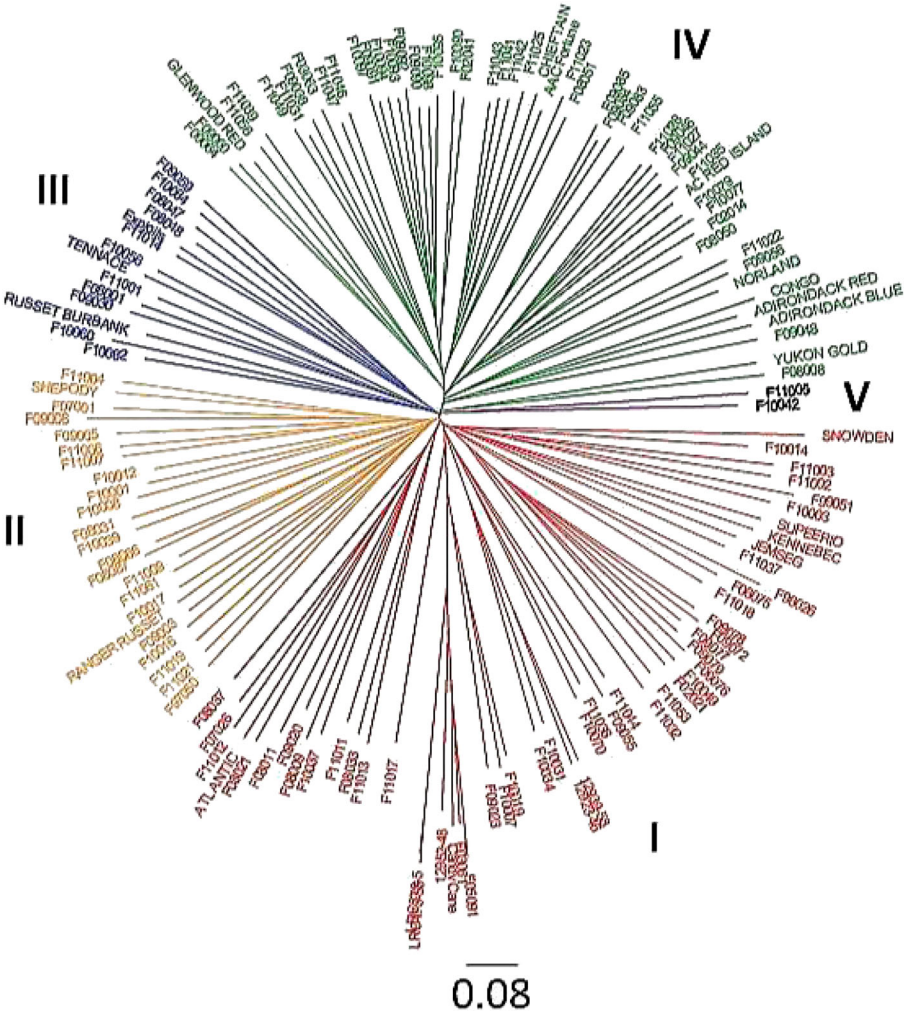

Fig. 2 Neighbour-joining tree of potato clones in the association panel. A total of five subpopulations were identified using PowerMarker (Liu and Muse 2005)

considering whether reference or alternative allele was dominant. The quantile-quantile (QQ) plots were generated by plotting the expected log *p* value against the observed values to test appropriateness of model to avoid false discovery caused by population stratification. The 1000 permutation method was used for establishing a *p* value detection threshold for statistical significance. The Manhattan plots were produced based on the vignette of GWASpoly with minor modification (Rosyara et al. 2016).

Results and Discussion

The phenotypic distribution of potato resistance to common scab in the study panel is presented in Fig. 1. The phenotypic distribution is continuous and slightly positively skewed. The estimated broad-sense heritability (h^2) for common scab resistance based on the data collected in 2012, 2014, and 2016 was 0.81. A total of 10,392 polymorphic SNPs from 12K SolCAP remained after filtering minor allele frequency (MAF < 0.05). These SNPs uniformly distributed across the 12 potato chromosomes were used in the GWAS.

Population Structure

The phylogenetic tree analysis using neighbour-joining method demonstrated the non-random distribution of genotypes within the association panel including the advanced breeding clones and commercial cultivars. The panel displayed both significant population structure and familial relationships and clustered into 5 distinct subpopulations (Fig. 2). The fixation index (F_{ST}), an assessment of population differentiation due to genetic structure, was around 0.16 suggesting a moderate differentiation of genetic structure within the association panel of clonal propagated crop. Among these five subpopulations, potato clones for processing were grouped into group I, II, III, and V

Table 1 The significant SNPs associated with potato common scab resistance

Model	Threshold	Marker	Chr	Position	MAF	SNP (X/Y*)	Score ($-\text{Log}_{10}$p)	Effect	Explained (%)
1-dom-alt	5.12	c2_17864	2	36550070	0.785	T/C	5.52	− 1.34	21
		cl_5844	2	36769707	0.213	A/G	NA		12
		c2_17867	2	36548178	0.643	A/G	2.29		8
General	5.29	cl_16291	4	1259748	0.456	A/G	5.76	NA	19
		c2_54791	4	1162713	0.811	T/C	0.32		6.6
2-dom-alt	5.2	cl_16291	4	1259748	0.456	A/G	7.02	− 1.81	19
2-dom-alt	5.2	c2_3251	12	9554964	0.403	T/C	6.24	− 1.94	26
		c2_3189	12	9518052	0.534	T/C	0.19		15
		c2_3247	12	9564388	0.227	A/C	NA		14

1-dom-alt: simplex-dominant-alternate allele models

2-dom-alt: duplex-dominant-alternate allele models

General: general models

*Allele associated with common scab resistance

while clones for fresh market were mostly clustered into group IV. Therefore, the diverged association panel in the NJ tree derived from potato genotypes indicated the pedigree closeness among these clones. Furthermore, these subpopulations also shared

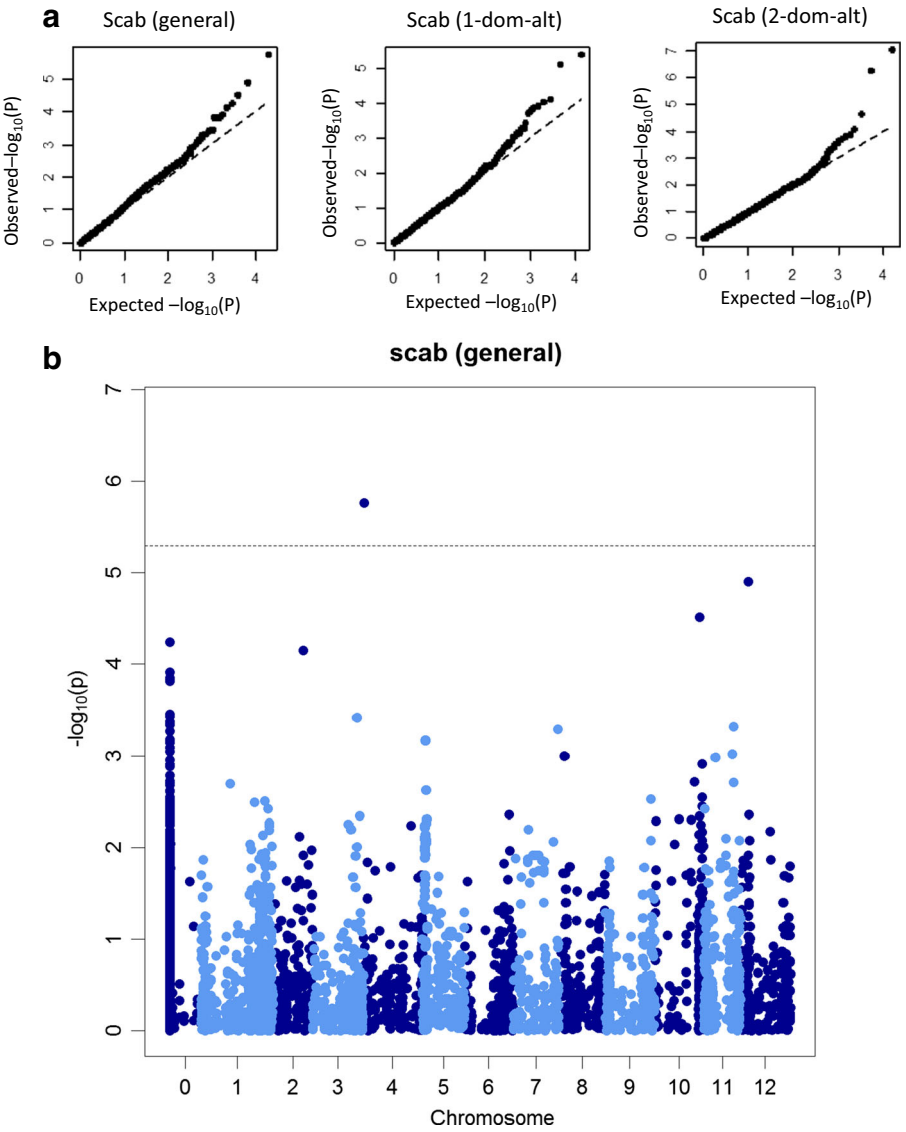

Fig. 3 QQ plots (**a**) and Manhattan plots of GWAS results (**b**–**d**) in the potato association panel. **a** QQ plots were generated under three models "general", "1-dom-alt", and 2-dom-alt", respectively, in the association panel. **b**–**d** Manhattan plots were generated using the $-\log_{10} p$ values from a genome-wide scan against the position on each of the 12 chromosomes in the association panel under these three models. The genome-wide significance threshold was marked by the horizontal line

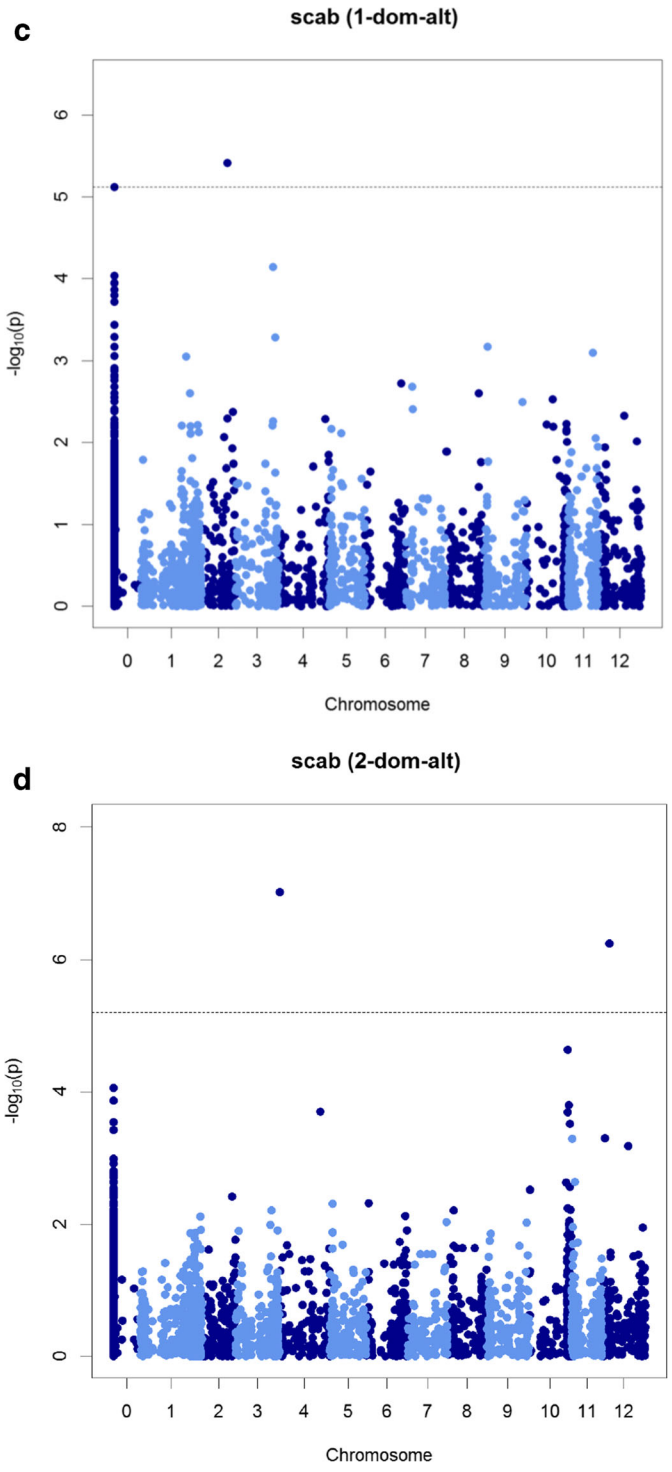

Fig. 3 continued.

similar clusters based on the market types suggesting that the genetic loci of these clones might be wedged by potato breeding effort, especially selection for the quality traits such as specific gravity, sugar, and starch content. Results of population structure analysis partially agree with Hirsch et al. (2013) and Deperi et al. (2018) who reported diversification of market classes resulting from long-term breeding process and divergent allele frequencies for SNPs related to processing traits such as carbohydrate metabolism.

GWAS Analysis

The association mapping analysis identified a total number of 211, 209, and 290 polymorphic SNP markers on chromosomes 2, 4, and 12, respectively, among 143 clones of the panel. Three QTLs defined by the significant SNPs for the common scab resistance were identified on chromosome 2, 4, and 12, respectively (Table 1; Fig. 3a). Three SNP markers (solcap_snp_c2_17864 (Chr2:36550070), solcap_snp_ c2_17867 (Chr2:36548178), and solcap_snp_c1_5844 (Chr2:36769707) underlying a QTL on chromosome 2 were identified using with the simplex-dominant-alternate allele (1-dom-alt) model. The proportions of phenotypic variation for potato resistance to common scab explained by those markers were 21%, 8%, and 12%, respectively (Table 1). The second QTL defined by two significant SNPs characterized by both general and duplex-dominant-alternate allele models was detected on chromosome 4 underlying solcap_snp_c1_16291 (Ch4: 1259748) and solcap_snp_c1_54791 (Ch4: 1162713). These markers explained 19% and 6.6% of the phenotypic variation, respectively. The third QTL was defined by three SNPs ((solcap_snp_c2_3251, Chr2:9554964), (solcap_snp_c2_3189, Chr2:9518026), and (solcap_snp_c2_3247, Chr2:9564388)) on chromosome 12 with the alternate allele of duplex dominant model gene action (Table 1). The solcap_snp_c1_16291 SNP on chromosome 4 was detected by two different (general and duplex-dominant-alternate) models. The

Table 2 Contribution of the first five principal components to the phenotypic variation in the association panel using prcomp algorithm in R program (www.r-project.org)

	PC1	PC2	PC3	PC4	PC5
Scab	−0.516	0.093	−0.360	0.070	−0.476
Bruising	−0.509	0.143	0.235	−0.286	0.508
Tuber blight	−0.063	0.022	−0.567	0.565	0.156
Specific gravity	−0.168	0.183	−0.424	−0.639	0.004
Early vigour	0.366	−0.041	−0.555	−0.251	0.345
Maturity	0.012	0.696	0.044	−0.020	−0.356
Top vigour	0.552	0.214	0.048	−0.196	−0.231
Total yield	0.065	0.636	0.041	0.290	0.438
Eigenvalue	1.276	1.249	1.154	1.058	0.853
Proportion of variance	0.203	0.195	0.166	0.140	0.091
Cumulative proportion	0.203	0.398	0.565	0.705	0.796

solcap_snp_c2_3251SNP marker of chromosome 12 explained the highest (26%) phenotypic variation of the resistance. Our results appear to confirm previous report by Alam (1972) that resistance to common scab requires the presence of a dominant allele at one locus and the presence of two homozygous recessive alleles at a second locus. In addition, we identified the location of the two recessive alleles at separate loci on chromosomes 4 and 12 as indicated by duplex-dominant-alternate allele models. However, not all SNPs passed the genome-wide significance threshold by GWASpoly software even though they explained a meaningful amount of phenotypic variation (Fig. 3b). Bradshaw et al. (2008) have previously identified two QTLs on chromosome 2 and 6 using AFLP and SSR markers via interval mapping with 227 clones derived from a cross of 12601ab1 and Stirling. The significant SNP marker mapped on the chromosome 2 in our study shared a similar location of the QTL with that of Bradshaw et al. (2008). Braun et al. (2017a, b) showed the presence of QTLs for common scab reaction expressed as the percentage of surface area covered with lesions and the lesion

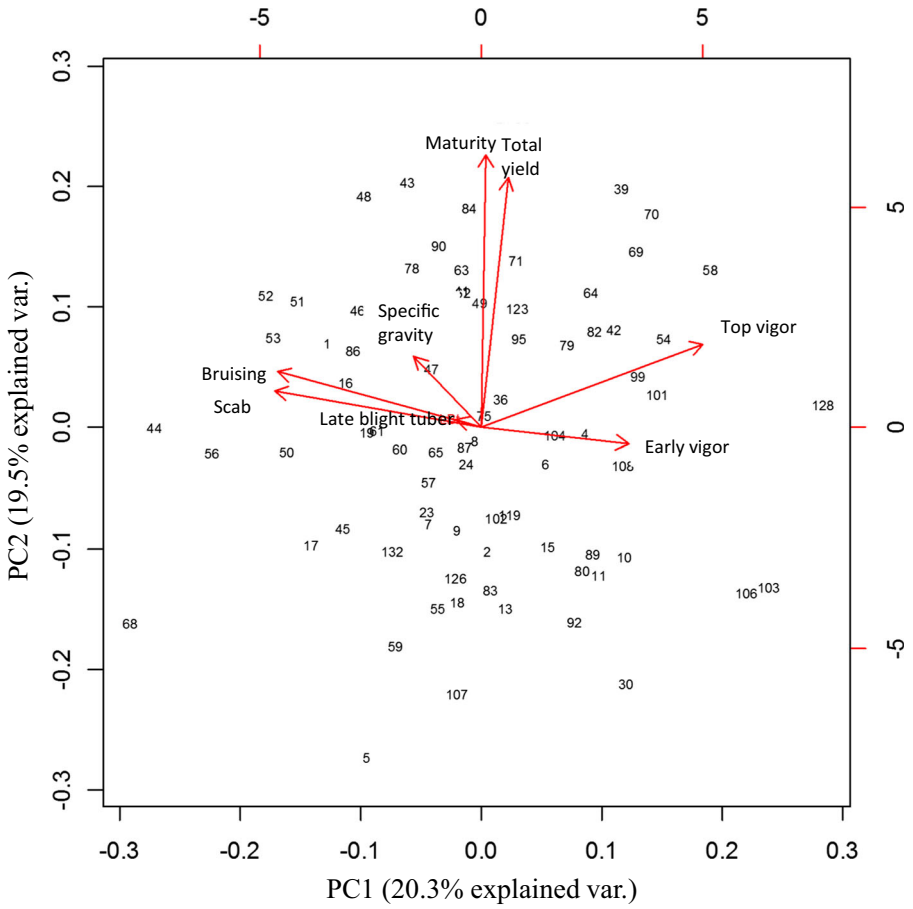

Fig. 4 PC1 vs. PC2 of association panel. gge bi-plot package was used to show the relationship among potato clones based on eight traits are shown by PCA

type, respectively, in a diploid population in the same location on chromosome 11 and these explained a large portion of phenotypical variation. None of the Braun et al. (2017a, b) QTLs was overlapping with those found in this study.

The QQ (quantile-quantile) plots of the genome-wide distribution of results (Fig. 3a) showed lower inflation of departure from the null hypothesis which indicates proper control of inflation caused by population structure or kinship. As displayed in the QQ plots of the expected distribution of the test statistics (*X*-axis) across the SNPs compared with the observed values (*Y*-axis) based on six mapping models, the nominal *p* values consistently show a solid line matching $X = Y$ until it sharply curves at the end against the distribution of observed $-\log_{10} p$ values from the mapping models.

The mechanism of potato resistance to the infestation of *S. scabies* is still not clearly understood (Braun et al. 2017a, b). It may also depend on the differences in pathogen isolates, inoculation method, cultivars, and location of the research plots (Loria et al. 2006; Koyama et al. 2006; Qu et al. 2008). In our study, potato cultivars showed almost a normal distribution (Fig. 1). Three genomic regions significantly associated with common scab resistance were identified. It is possible that these regions harbour other important traits. An association of scab reaction with fry colour was also reported by Bradshaw et al. (2008), indicating possible linkage or pleiotropic effects. Using principal component analysis, scab was found to be correlated with specific gravity (a major market class differentiation trait), and both traits were found to have negative projection on the first principal component and positive projection on the second principal component (Table 2). The first two PCs were visualized in a biplot using ggbiplot package (Fig. 4). Graphical representation revealed that scab and specific gravity were grouped into similar direction, indicating a relationship of these traits as found in the PCA. This study was conducted on single-SNP association analysis. A number of studies have shown that combining single SNP markers into haplotypes can provide greater QTL detection power and mapping accuracy than single SNP markers in genome-wide association, in addition to capturing epistatic interaction (He et al. 2011; N'Diaye et al. 2017).

Conclusions

Significant SNPs for potato common scab resistance were identified using GWAS on potato chromosomes 2, 4, and 12 in an association panel composed of advanced potato clones and commercial cultivars. These findings showcase the importance of high-resolution genome-wide association mapping to decipher complex quantitative disease-resistant traits in potato. These findings will be useful to design marker-assisted selection and breeding strategies to improve resistance to common scab and overall performance in new potato cultivars.

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