Quantitative Trait Loci for Resistance to Common Scab and Cold-Induced Sweetening in Diploid Potato

Sarah R. Braun, Jeffrey B. Endelman, Kathleen G. Haynes, and Shelley H. Jansky*

Abstract
The development of germplasm with resistance to common scab and cold-induced sweetening is a high priority for the potato (Solanum tuberosum L.) industry. A mapping population was developed from mating two individuals of a diploid family generated by crossing the susceptible cultivated potato clone US-W4 to the highly resistant wild relative (Solanum chacoense Bitter) clone ‘524–8’. Progeny were evaluated in replicated field trials. Tubers were scored for percentage of surface area with scab lesions, scab lesion type, cold-induced sweetening, average tuber weight, and dry matter. Plants were evaluated for vine maturity. A genetic map was constructed, quantitative trait loci (QTLs) were identified, and the gene action of significant QTLs was characterized using 1606 single nucleotide polymorphisms (SNPs). Significant QTLs for common scab percentage of surface area covered with lesions and lesion type were identified in overlapping regions on chromosome 11 ($R^2 = 21.0$ and 18.2%, respectively). Quantitative trait loci were identified on chromosomes 4 ($R^2 = 17.1$%) and 6 ($R^2 = 19.4$%) for cold-induced sweetening, chromosome 5 for maturity ($R^2 = 29.8$%), and chromosome 1 ($R^2 = 26.3$ and 22.0%) for average tuber weight. Identification of QTLs is the first step toward developing molecular markers for breeders to efficiently integrate these desirable traits into cultivars.

Core Ideas
- Resistance to common scab and cold-induced sweetening is important to the potato industry.
- A quantitative trait locus (QTL) for resistance to common scab was identified on chromosome 11.
- Two QTLs for resistance to cold-induced sweetening were identified on chromosomes 4 and 6.
- Additional QTLs were detected for vine maturity and tuber weight.
- This is the first step in the development of molecular markers for use by breeders.

Potato common scab is a widespread disease that causes scablike lesions on tubers in many production regions worldwide. It can result in a substantial reduction in marketable yield for potato growers (Loria, 2001). Common scab is caused by the soilborne bacterial pathogen Streptomyces scabies (Thaxt.) Waksman and Henrici. The pathogen produces the phytotoxin thaxtomin A, causing lesions on tuber surfaces (Tegg and Wilson, 2010). In addition to scab lesions, cold-induced sweetening (CIS) also has a major impact on potato’s marketable yield. The

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potato processing industry requires tubers that produce light-colored fry products at harvest and after cold storage. Most potato cultivars exhibit CIS, which occurs when tubers are stored at temperatures below 10°C (Sowokinos, 2001). Tubers from these cultivars produce dark products when fried, mainly because of the accumulation of the reducing sugars glucose and fructose. Cultivars that combine resistance to common scab and CIS would be highly desirable for the potato industry.

High levels of resistance to common scab and CIS are not found in most commercially significant cultivars of potato. However, the wild tuber-bearing diploid potato relative *S. chacoense* has been identified as a source of resistance to these traits (Dionne and Lawrence, 1961; Douches and Freyre, 1994; Hosaka et al., 2000; Hamernik et al., 2009; McCann et al., 2010). Diploid derivatives of *S. tuberosum* are sexually compatible with *S. chacoense* (Hermundstad and Peloquin, 1986). Sexual polyploidization can then be used to return to the tetraploid level (Ortiz et al., 2009). In fact, *S. chacoense* is credited with making major contributions to processing quality in modern tetraploid potato cultivars (Love et al., 1998).

Major gene models have been proposed for resistance to common scab and CIS. Scab resistance was reported to be conferred by two loci, one dominant and one recessive (Alam 1972; Murphy et al., 1995). Gene models for resistance to CIS propose two loci for chip color stability at low temperatures (Lynch et al., 2003) and three loci for reconditioning and reversion resistance (Thill and Peloquin, 1994). Bhaskar et al. (2010) were able to control CIS by suppressing one gene (the vacuolar invertase gene) that catalyzes the cleavage of sucrose into glucose and fructose. Genetic studies of resistance to common scab and CIS are challenging to carry out because the environmental influence on phenotype is large (Wiersema, 1974; Xiong et al., 2002; Bradshaw et al., 2008; McCann et al., 2010). Consequently, replicated trials in multiple environments are required to assign phenotypes accurately.

The recent availability of the SNPs array developed by the Solanaceae Coordinated Agricultural Project (SolCAP) has enabled genetic analysis in potato with broad and dense genome coverage (Hamilton et al., 2011; Felcher et al., 2012). Thus genotypic information may now be gathered efficiently for populations segregating for traits of interest, such as scab and CIS resistance. Quantitative trait locus analysis can then be performed to associate phenotypic variation with genotypic variation (Broman and Sen, 2009). To date, one study has identified QTLs for resistance to scab, in tetraploid cultivated potato (Bradshaw et al., 2008). Quantitative trait loci for CIS have been found on several chromosomes in diverse populations (Douches and Freyre, 1994; Menendez et al., 2002; D’hooop et al., 2008; Soltys-Kalina et al., 2015).

In addition to identifying the chromosomal regions responsible for resistance phenotypes, QTL analyses can estimate the gene action of those regions. The effect of an allele is the average change in the phenotype when one allele is substituted for the other allele. If the gene action is additive, then the effect of the allelic substitution is equal to the additive effect, *a*, which is the difference between one homozygous genotype and the average of the two homozygous genotypes. The degree of dominance (*d*) between alleles is measured by taking the difference between the value of the heterozygote and mean of the homozygotes. The dominance ratio (*d/a*) quantifies the level of dominance of a QTL (Fehr, 1991).

The purpose of this study was to identify QTLs in a diploid *F₂* population derived from a cross between the cultivated potato (*S. tuberosum*) clone US-W4 and the wild relative (*S. chacoense*) clone 524–8. The population was developed to study segregation for resistance to common scab and CIS, but it was also phenotyped for other segregating traits, including vine maturity, dry matter, and average tuber weight (ATW).

### Materials and Methods

#### Population Development and Phenotyping

The *F₂* population was derived by intersecing two randomly chosen full-sib progeny of the *S. tuberosum* dihaploid US-W4 (*2n = 2x*) and clone 524–8, an *S7* inbred line of the diploid wild species *S. chacoense*. US-W4 is susceptible to common scab and CIS, and has early vine maturity, low plant vigor, and moderate ATW. It was produced via parthenogenesis from the tetraploid University of Minnesota breeding line ‘MN 20–20–34’ developed by F. Krantz. Because US-W4 originated from a partially inbred tetraploid clone via parthenogenesis, it is somewhat homozygous. Of 8091 SNPs evaluated on the SolCAP Illumina array, 64.8% are homozygous. Clone 524–8 has consistently demonstrated resistance to common scab and CIS, and has late vine maturity, high plant vigor, and low tuber weight. It has been self-pollinated for seven generations and is homozygous for 89.0% of 7817 SolCAP SNPs.

Seed tubers of the *F₂* clones and their parents and grandparents were generated in a greenhouse for use in replicated field trials. Two seed tubers were planted per plot and all phenotypic evaluations were done on a plot basis. In 2011 and 2012, a randomized complete block design consisting of two blocks was planted at the Langlade Research Station (Antigo, WI), in a field that is maintained for high scab disease pressure. In 2011, the field was planted on 25 May and harvested on 3 October. In this trial, 48 of the 99 *F₂* clones were planted in one replication per block. In 2012, the field was planted on 11 May and harvested on 2 October. In this trial, 91 clones were evaluated with three replications in each block. All plots were evaluated for vine maturity on 9 Sept. 2011 and 22 Aug. 2012. The maturity scale ranged from 1 to 5 where 1 = dead or nearly so; 2 = prostrate with some dead stems; 3 = partially upright, mostly after flowering; 4 = full flowering; 5 = preflowering. In 2015, a randomized complete block design consisting of two blocks was planted at the Hancock Agricultural Research Station (Hancock, WI). The 2015 Hancock field was planted on 5 May and harvested on 21 September. This trial included 66 of the *F₂* clones.
The 10 largest tubers from each plot (or all tubers if less than 10 were available) were washed and visually scored for scab. Two measures were used: (i) percentage of tuber surface area with lesions (PSA), on a scale of 0 to 100% in increments of 5%, and (2) lesion type (LT), using the scale 0 = no lesions, 1 = superficial and small, 2 = superficial and coalescing, 3 = raised and small, 4 = raised and coalescing, 5 = pitted and small, 6 = pitted and coalescing. For the QTL analyses of PSA and LT, all scored tubers within a plot were averaged. Percentage of surface area and LT were scored separately because the correlation between these two traits is variable, ranging from 0.30 to 0.93 (Bjor and Roer, 1980; Loria, 1981; Lambert et al., 2006).

Tubers were kept at room temperature (22°C) for 14 to 21 d after harvest while they were scored for scab. Tubers from the field trials were then placed in a cooler at 4°C for 62 to 78 d. After cold storage, the four largest tubers from each plot were weighed to provide the ATW score. Two of the four tubers were cut in half from stem to bud end, and a 4-mm slice from each tuber was fried in vegetable oil at 191°C and visually evaluated on a scale from 1 (very light) to 10 (very dark).

Statistical Analysis

Genetic correlations among the three environments (Antigo-2011, Antigo-2012, and Hancock-2015) were estimated with the following linear model, using SAS PROC MIXED version 9.4 (SAS Institute Inc., Cary, NC):

\[ y_{ijk} = \mu + b_i + g_e + g_{jk} + \varepsilon_{ijk} \]  

[1]

In Eq. [1], \( y_{ijk} \) is the phenotype for genotype \( j \) in block \( i \) of environment \( k \), \( b_i \) is the block effect, \( g_e \) is the main effect for environment, and \( g_{jk} \) is the genotype effect within environment \( k \) (i.e., the “G + GE” effect). The variance of the residual effect \( \varepsilon \) was modeled as environment-specific using the REPEATED command in PROC MIXED. The \( g_{jk} \) effect was random with a separable covariance structure, \( \text{Var}[g_{jk}] = I \otimes \Sigma \), where \( \Sigma \) is the unstructured \( 3 \times 3 \) genetic covariance matrix between the environments. All residuals were examined for normality and treated with the potato 8303 SNP array (Hamilton et al., 2011; Felcher et al., 2012). Hierarchical clustering (hclust in the R package) revealed that five of the samples were duplicates, which were removed to give 105 unique genotyped progeny. Fewer progeny were used in the phenotype analyses than the genotype and mapping analyses because of tuber seed source attrition.

DNA for 110 F₂ progeny was extracted using the cetyl(trimethyl)ammonium bromide protocol and genotyped with the potato 8303 SNP array. Genetic Mapping

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In a sib-mated F₂ population, there are three categories of codominant SNP markers (Maliepaard et al., 1997). Markers can be heterozygous in both F₁ parents (“F₂-type”, 1:2:1 expected ratio), heterozygous in the female parent and homozygous in the male parent (“BC-type”, 1:1 expected ratio), or heterozygous in the male parent and homozygous in the female parent (“BC-type”, 1:1 expected ratio). As our goal was to estimate QTL effects relative to the grandparents US-W4 and 524–8, neglecting potential differences in the size of the effect between the two QTL alleles within each grandparent, we focused on the F₂-type markers. With only one parental genotype available (the other was lost during maintenance of the population), we used the χ² goodness-of-fit test for the 1:2:1 distribution to identify putative F₂-type markers. A bimodal distribution of p-values was observed (Supplemental Fig. S1), with the two modes interpreted as corresponding to the F₂- and BC-type markers. Based on this distribution, a threshold of \( p > 10^{-4} \) was used to identify putative F₂ markers. Since the use of a p-value threshold has the potential to exclude chromosome regions showing high segregation distortion, the genomewide distribution of the putative F₂ markers was inspected (Supplemental Fig. S2). No large gaps were observed but after inspection of the preliminary genetic map, two additional markers with \( p = 10^{-7} \) were added to fill out the map on chromosome 10.

The F₂-type markers can be further subdivided into five nonredundant categories (A × B, A × H, H × A, H × H, and H × B) based on the grandparental genotype combination (524–8 × W4), where A and B denote the two homozygous states and H is heterozygous. Because of the inbred nature of the 524–8 grandparent, 1464 of the 3116 markers were either A × B or A × H types, which provided adequate genomewide coverage, except on chromosomes 8 and 12 (Supplemental Fig. S2). These two chromosomes have higher than expected residual heterozygosity. By including the H × B and H × A marker types, adequate genomewide coverage was achieved.
One of the attractive features of using inbred grandparents for an F₁ population is that genotype calls based on the marker state are equivalent to coding by grandparent descent. This property means that phase relationships are known a priori and color-coded genotypes can be ordered by visual inspection (e.g., with Microsoft Excel or specialized software; Young and Tanksley 1989; van Berloo 1999). For a sib-mated F₂ population, the A × B, A × H, and H × B marker types also have an equivalency between state and descent-coded genotypes. The H × A types can be grouped with the previous three on inverting the marker encoding (i.e., using the transformation y = 2 – x for genotypes coded x = 0,1,2). For markers of type H × H, there is not a priori relationship between the state and descent encodings and thus they were not used.

Markers were divided into linkage groups and initially ordered using version 4.03 of the potato reference genome (The Potato Genome Sequencing Consortium, 2011; Sharma et al., 2013), which has been reported to have high but not perfect fidelity in several studies (Prashar et al., 2014; Massa et al., 2015; Endelman and Jansky 2016). Markers were locally reordered by visual inspection as needed or removed when it was clear they did not fit. In addition, six progeny were removed because they had excessive missing data or problems with data quality (i.e., too many apparent recombinations). On the basis of this fixed order, a final linkage map of 1606 markers and 99 progeny was created with custom R scripts, using Kosambi’s map function and the logarithm of odds (LOD)-score-weighted least-squares criterion (Stam 1993; Liu 2002). Discrepancies with the reference genome were small and concentrated in the pericentromeric regions (Supplemental Fig. S3), similar to the results of Endelman and Jansky (2016). The marker data and genetic map are provided in Supplemental Table S1, with genotypes coded 0,1,2 for the dosage of the W4 alele.

Quantitative trait locus analysis was conducted in R using the qtl package with Haley–Knott regression (Broman and Sen, 2009). The percentage of phenotypic variance explained by the QTLs was calculated from the equation 1 – 10⁻²LODα for traits with a single QTL. The LOD significance threshold for each trait was based on 1000 permutations, with a false positive rate of α = 0.05. If more than one QTL was detected, then a multiple QTL model was implemented and the LOD values and the percentage of phenotypic variance explained by the QTLs were reported from the model using the scantwo function. The flanking markers of significant QTLs were calculated with an approximate Bayesian credible interval at 95%. The effect of an allelic substitution and dominance ratio was calculated as d/a using fitqtl in R/qtl.

**Results**

**Phenotypic Analysis and Heritability of Traits**

Broad-sense heritability estimates varied across traits (Table 1). Scab LT was moderately high and consistent across individual environments (0.60–0.72) compared with scab PSA, which was moderately high in 2012 (0.79) but relatively lower in 2011 and 2015 (0.54, 0.48). Like LT, CIS was moderately high for all environments (0.56–0.72), but slightly lower in 2015 (0.56). Vine maturity had the greatest difference in heritability between years, as it was high in 2012 (0.91) but lower in 2011 (0.54). High heritabilities were also observed for ATW in 2012 and 2015 (0.81, 0.83) compared with 2011 (0.69). Dry matter, like LT, was relatively consistent across environments (0.63–0.69).

Strong correlations were detected between 2012 and 2015 for PSA (0.83) and LT (0.72), among all three environments for CIS (1.00, 0.88, 0.93) and ATW (0.70, 0.90, and 0.84), and between 2011 and 2012 for dry matter (0.84) (Table 2). All other correlations between years for each trait were less than 0.64. The phenotypes from years with the strongest correlation for a trait were used to generate the BLUP for the trait used in the QTL analysis (Table 2, Supplemental Table S2). In the case of ATW, the strongest phenotypic correlation was between 2011 and 2015. Since the greatest number of clones was tested in 2012, and the correlations between the other years and 2012 were relatively high, the QTL analyses were conducted with the BLUPs calculated with 2011 and 2012 data as well as BLUPs with 2012 and 2015 data. Pearson correlations between traits also varied, and only PSA and LT had a strong correlation (r > 0.70). Frequency diagrams of the traits among environments may be referenced in Supplemental Fig. S4.

**Genetic Map and QTL Analysis**

The total genetic map length was 822 cM, which was within the range of previous studies (606–1120 cM) in diploid populations generated from wild and cultivated potato species (Bonierbale et al., 1988; Jacobs et al., 1995; Endelman and Jansky, 2016). A single QTL on chromosome 11 was detected for common scab PSA (Table 3), which explained 21.0% of the phenotypic variance in the population. A QTL for common scab LT was detected 6.2 cM away from the PSA QTL on chromosome 11, explaining 18.2% of the phenotypic variance. Significant QTLs for CIS were detected on chromosomes 4 and 6. Each QTL explained just under 20% of the variation individually; when QTLs were combined the R² value for the model was 44.8%. The most significant QTL in this study

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**Table 1. Broad-sense heritability on an entry-mean basis for the six potato traits measured in this study, for each of the three environments.**

<table>
<thead>
<tr>
<th>Trait</th>
<th>2011</th>
<th>2012</th>
<th>2015</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage of surface area</td>
<td>0.54</td>
<td>0.79</td>
<td>0.48</td>
</tr>
<tr>
<td>Lesion type</td>
<td>0.72</td>
<td>0.67</td>
<td>0.60</td>
</tr>
<tr>
<td>Cold-induced sweetening</td>
<td>0.63</td>
<td>0.72</td>
<td>0.56</td>
</tr>
<tr>
<td>Vine maturity†</td>
<td>0.54</td>
<td>0.91</td>
<td>–</td>
</tr>
<tr>
<td>Average tuber weight</td>
<td>0.69</td>
<td>0.81</td>
<td>0.83</td>
</tr>
<tr>
<td>Dry matter</td>
<td>0.64</td>
<td>0.69</td>
<td>0.63</td>
</tr>
</tbody>
</table>

† Vine maturity was not measured in 2015.
Table 2. Genetic correlation between environments for the percentage of surface area (PSA) and lesion type (LT) of common scab, cold-induced sweetening (CIS), vine maturity (VM), average tuber weight (ATW), and dry matter (DM) in potato.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Year</th>
<th>Year</th>
<th>Correlation</th>
<th>Years used for quantitative trait locus mapping</th>
</tr>
</thead>
<tbody>
<tr>
<td>PSA</td>
<td>2011</td>
<td>2012</td>
<td>0.62</td>
<td>2012 &amp; 2015</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>0.83</td>
<td></td>
</tr>
<tr>
<td>LT</td>
<td>2011</td>
<td>2012</td>
<td>0.54</td>
<td>2012 &amp; 2015</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>0.72</td>
<td></td>
</tr>
<tr>
<td>CIS</td>
<td>2011</td>
<td>2012</td>
<td>1.00</td>
<td>2011 &amp; 2012</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>0.93</td>
<td></td>
</tr>
<tr>
<td>VM</td>
<td>2011</td>
<td>2012</td>
<td>0.48</td>
<td>2012</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>NA†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>NA†</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>0.90</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>0.84</td>
<td></td>
</tr>
<tr>
<td>DM</td>
<td>2011</td>
<td>2012</td>
<td>0.84</td>
<td>2011 &amp; 2012</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>2015</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>2015</td>
<td>0.08</td>
<td></td>
</tr>
</tbody>
</table>

† NA, not applicable, since vine maturity was not measured in 2015.

diplodloid clone *S. tuberosum* US-W4 is moderately inbred and the resistant diploid clone *S. chacoense* 524–8 is highly inbred. It was possible to generate a sib-mated *F₂* population and use that structure in the mapping protocol. This is unique in potato, which is typically self-incompatible at the diploid level and, consequently, highly heterozygous. A single significant QTL for resistance to common scab was found on chromosome 11 (Table 3). Bradshaw et al. (2008) identified two QTLs for scab resistance in a tetraploid cultivated potato population, but no single QTL explained greater than 8.2% of the phenotypic variance. The QTLs in the Bradshaw et al. (2008) study were located on chromosomes 2 and 6. Resistance in our study is probably controlled by different genes than those in the Bradshaw et al. study, since resistance was localized to different chromosomes and did not originate from the same germplasm source.

Variation in heritability and correlations across years for a trait is probably partly caused by differences in the number of replications and the number of *F₂* clones available for each trial. In 2011, the screen consisted of two replications per genotype in the field but there was only enough seed to evaluate 48 of the 99 *F₂* clones. This is in contrast to 2012, where six replications for each of 91 *F₂* clones were present in the field. In 2015, the trial was planted at a different site with scab pressure, for which there was enough seed for two replications of 66 of the clones. Heritability estimates for common scab in the literature are variable, ranging from high values of 0.83 to 0.89 (Haynes et al., 1997; Navarro et al., 2015), to moderate values of 0.64 to 0.66 (Bradshaw et al., 2008; Zorrilla et al., 2014), and values as low as 0.18 to 0.34 (Haynes et al., 2009; Zorrilla et al., 2014). In this study, heritability...
Fig. 1. Effect of allelic substitution on quantitative trait loci (QTLs) for percentage of tuber surface area (PSA) covered with scab lesions, scab lesion type (LT), cold-induced sweetening (CIS), vine maturity (VM), and average tuber weight (ATW). The standard error of the mean at each genotype is represented by the by the “+” signs. “AA” represents the *S. chacoense* 524–8 grandparent and “BB” represents the *S. tuberosum* US-W4 grandparent.
estimates for common scab ranged from 0.52 to 0.74, with LT having greater heritability estimates (Table 1).

Haynes et al. (1997) discussed the importance of using new germplasm sources to develop potato clones with stable, high levels of resistance to scab. The S. chacoense clone 524–8 is an inbred line of a diploid wild tuber-bearing potato relative. This clone has consistently displayed resistance to common scab across environments, based on measurements of both PSA and LT. It has also regularly displayed resistance to CIS. Solanum chacoense crosses readily with diploid cultivated potato to produce offspring with acceptable tuber type (Jansky et al., 1990). In fact, S. chacoense has been an important germplasm source for the improvement of processing cultivars (Love et al., 1998). In this study, S. chacoense contributed dominant alleles for resistance to CIS, but toward scab resistance, it contributed additive (PSA) or recessive (LT) alleles. It will be difficult to fix a recessive allele in tetraploid germplasm. However, major efforts to convert potato to a diploid inbred line-based crop are underway in Europe (Lindhout et al., 2011) and North America (Jansky et al., 2016). This new breeding strategy would allow breeders to incorporate recessive traits into cultivars.

The finding of a single QTL for scab resistance indicates that there is at least one locus that controls scab resistance in our germplasm source, S. chacoense 524–8. Previous studies have proposed two major loci controlling scab resistance in potato (Alam 1972; Murphy et al., 1995). In studies based on S. tuberosum as a resistance source, resistance appears to be a dominant trait (Bradshaw et al., 2008; Haynes et al., 2010). Resistance based on S. chacoense exhibits incomplete dominance (Dionne and Lawrence, 1961). In our S. chacoense 524–8-derived germplasm, scab susceptibility appears to be a partially dominant trait, with LT being closer to dominant and PSA closer to additive (Table 3, Fig. 1). It is interesting to note that in Arabidopsis thaliana (L.) Heynh., a single recessive mutation at a nuclear locus results in reduced uptake of the Streptomyces pathogenicity factor thaxtomin (Scheible et al., 2003). It may be worth examining this locus as a candidate gene for resistance to scab.

A strong correlation (r = 0.75) was identified between PSA and LT. Similar relationships have been reported previously, and range from 0.30 to 0.77 (Björ and Roer, 1980), 0.80 to 0.93 (Loria 1981), and 0.85 (Lambert et al., 2006). Quantitative trait loci in the same region of chromosome 11 were discovered for both traits, raising the possibility that a single locus affects disease severity and LT for common scab.

A QTL associated with chip color after cold storage (a measure of CIS) was detected on chromosomes 4 and 6 (Table 3). In other studies, QTLs for chip color after cold storage have been reported (Douches and Freyre, 1994; Menendez et al., 2002; Gebhardt et al., 2005; Li et al., 2005; Bradshaw et al., 2008). However, in each of these studies, several QTL were identified. In contrast, Soltys-Kalina et al. (2015) identified two QTL in a potato diploid mapping population: one on chromosome 1 and another on chromosome 6. We have identified two QTLs that, when considered together, explain 44.8% of the phenotypic variation for chip color in 524–8-derived germplasm. In our population, the QTL for CIS resistance on chromosome 4 is closer to additive (dominance ratio = –0.17) (Table 3, Fig. 1). Douches and Freyre (1994) also identified markers associated with chip color on chromosome 4 and suggested that additive effects are important for chip color variation after cold storage. It is possible that the loci for CIS resistance in our study are those reported by Douches and Freyre (1994), especially since they were also mapping in germplasm derived from hybrids between S. tuberosum and S. chacoense. Resistance to CIS is a partially dominant trait. The QTL for resistance to CIS on chromosome 6 is partially dominant (Table 3, Fig. 1). Bradshaw et al. (2008) reported that both dominant and recessive alleles for resistance to CIS are present on chromosome 6 in European cultivars.

We also identified a QTL on chromosome 5 that explained 29.8% of the phenotypic variance for vine maturity (Table 3). In previous studies in tetraploid S. tuberosum, QTLs for vine maturity were also identified on chromosome 5 (Bradshaw et al., 2008; McCord et al., 2011a, 2011b). Others have identified a major QTL for vine maturity on chromosome 5 in diploid populations with wild species in the pedigree (van den Berg et al., 1996; Collins et al., 1999; Visker et al., 2005; Kloosterman et al., 2013; Manrique-Carpintero et al., 2015). Recent genetic advances using diploid populations have allowed researchers to determine that a major regulator gene is responsible for the plant maturity QTL on chromosome 5 (Kloosterman et al., 2013). This gene is a transcription factor that regulates the length of the life cycle and tuber initiation.

A QTL for ATW was identified on chromosome 1 (Table 3). Manrique-Carpintero et al. (2015) also identified a QTL for ATW on chromosome 1, although other QTL had higher LOD values on different chromosomes, with the greatest on chromosome 5. Alleles from cultivated S. tuberosum US-W4 were dominant over those from wild S. chacoense 524–8 (dominance ratio = 0.82 and 1.07) (Table 3; Fig. 1). Wild Solanum species produce small tubers, typically 0.5 to 2.0 cm in diameter (Spooner et al., 2004). Cultivated potato produces a smaller number of larger tubers. Consequently, the large tuber size in cultivated potato is a major domestication trait. Significant modifications in tuber size in various transgenic lines have resulted from the overexpression of either a cytosolic or an apoplastic invertase gene or the use of an AGPase antisense background (Taubberger et al., 1999). AGPase antisense plants produce increased tuber number and decreased tuber size. After overexpressing an apoplastic invertase gene, the plants had fewer tubers in the large size category.

Conclusions
For the past 15 yr, a major research thrust in the potato genetics community has been the development of genetic...
maps, but major QTLs for resistance to common scab have not been reported. We have identified genomic regions associated with resistance to common scab and CIs in a highly resistant germplasm source. *S. chacoense* 524–8 exhibits high levels of resistance to both traits, so it is an exceptional source of genes for breeders and other researchers interested in studying plant–pathogen interactions and tuber carbohydrate physiology. In addition, this clone crosses readily with cultivated potato, allowing the introgression of resistance genes into advanced breeding lines and their expression in a genetic background that is relevant to breeding programs. The combination of germplasm with exceptional resistance to two critical industry challenges, common scab and CIs, along with the development of molecular markers to follow the relevant genomic regions, will accelerate breeding progress toward the development of superior cultivars.

**Supplemental Information**

Supplemental information is available for this article.

**Conflict of Interest Disclosure**

The authors declare that there is no conflict of interest.

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**References**


