3-1-2023

# Two QTLs govern the resistance to Sclerotinia minor in an interspecific peanut RIL population

Melina H. Rosso
*Criadero El Carmen S.A.*, mrosso@criaderoelcarmen.com.ar

Francisco J. de Blas
*Instituto de Botanica del Nordeste*

Alicia N. Massa
*USDA ARS National Peanut Research Laboratory*

Claudio Oddino
*Criadero El Carmen S.A.*

Damian F. Giordano
*Universidad Nacional de Rio Cuarto*

*See next page for additional authors*

Received: 21 April 2022 | Accepted: 25 October 2022 | Published online: 19 January 2023

DOI: 10.1002/csc2.20875

Crop Science

ORIGINAL ARTICLE

Crop Breeding & Genetics

# Two QTLs govern the resistance to *Sclerotinia minor* in an interspecific peanut RIL population

**Melina H. Rosso**[1,#] | **Francisco J. de Blas**[2,3,#] | **Alicia N. Massa**[4] | **Claudio Oddino**[1,5] | **Damian F. Giordano**[5] | **Jose G. Seijo**[6] | **Renee S. Arias**[4] | **Juan H. Soave**[1] | **Sara J. Soave**[1] | **Mario I. Buteler**[1] | **Marina Bressano**[7]

[1]Criadero El Carmen S.A., Cabrera, Córdoba, Argentina

[2]Univ. Nacional del Nordeste (UNNE), Consejo Nacional de Investigaciones en Ciencia y Tecnología (CONICET), Instituto de Botánica del Nordeste (IBONE), Corrientes, Argentina

[3]Facultad de Ciencias Agropecuarias Univ. Nacional de Córdoba (FCA – UNC), Córdoba, Argentina

[4]USDA-ARS-National Peanut Research Lab. (NPRL), Dawson, Georgia, USA

[5]Facultad de Agronomía y Veterinaria, Univ. Nacional de Río Cuarto (FAV-UNRC), Córdoba, Argentina

[6]Facultad de Ciencias Exactas y Naturales y Agrimensura, Univ. Nacional del Nordeste (UNNE), Consejo Nacional de Investigaciones en Ciencia y Tecnología (CONICET), Instituto de Botánica del Nordeste (IBONE), Corrientes, Argentina

[7]Biología Celular, Facultad de Ciencias Agropecuarias, Univ. Nacional de Córdoba, Córdoba, Argentina

**Correspondence**
Melina H. Rosso, Criadero El Carmen S.A, Bv. Italia 835, CP 5809, Gral. Cabrera, Córdoba, Argentina.
Email: mrosso@criaderoelcarmen.com.ar

Francisco J. de Blas, Univ. Nacional del Nordeste (UNNE), Consejo Nacional de Investigaciones en Ciencia y Tecnología (CONICET), Instituto de Botánica del Nordeste (IBONE), Sargento Juan Bautista Cabral 2131 3402BKG Corrientes, Argentina.
Email: fdeblas@agro.unc.edu.ar

Assigned to Associate Editor Francisco Gomez.

**Funding information**
Agricultural Research Service; Universidad Nacional de Córdoba; Criadero El Carmen S.A; Consejo Nacional de Investigaciones Científicas y Técnicas

## Abstract

Sclerotinia blight is a soilborne disease caused by *Sclerotinia minor* Jagger and can produce severe decrease in yield. Cultural management strategies and chemical treatment are not completely effective; therefore, growing peanut-resistant varieties is likely to be the most effective control method for this disease. Sclerotinia blight resistance has been identified in wild *Arachis* species and further transferred to peanut elite cultivars. To identify the genome regions conferring Sclerotinia blight resistance within a tetraploid genetic background, this study evaluated a population of recombinant inbred lines (RIL) with introgressed genes from three wild diploid species: *A. cardenasii*, *A. correntina*, and *A. batizocoi*. Two consistent quantitative trait loci (QTLs), *qSbIA04* and *qSbIB04* located on chromosomes A04 and B04, respectively, were identified. The QTL *qSbIA04* was mapped at 56.39 cM explaining 29% of the phenotypic variance and *qSbIB04* was mapped at 13.38 cM explaining 22% of the overall phenotypic variance.

**Abbreviations:** bp, base pairs; cM, centimorgan; DAS, days after sowing; DGC, Di Rienzo, Guzmán, and Casanoves test; DNA, deoxyribonucleic acid; H-K, Haley-Knott; LG, linkage group; LOD, log odds; PVE, phenotypic variation explained; QTL, quantitative trait loci; RIL, recombinant inbred line; SNP, single nucleotide polymorphisms; ssp, species; Tn, tons.

[#]Melina H. Rosso and Francisco J. de Blas have contributed equally.

## 1 | INTRODUCTION

Peanut (*Arachis hypogaea* L.) is an important allotetraploid (AABB) oilseed crop cultivated in more than 100 countries worldwide; however, 70% of the production is concentrated in China with approximately 17 million Tn (41%), India with 6 million Tn (14%), Nigeria (7.4%), United States (7.4%), and ranking fifth Argentina (2.8%) (SAGPyA, 2020), of which it exports 90% of its production (FAOSTAT, 2019).

In peanut production areas throughout the world, the diseases caused by soil pathogens generate large yield losses (Isleib & Wynne, 1992; Marinelli et al., 2017; Porter et al., 1982). Sclerotinia blight is one of the most important soilborne diseases (Faske et al., 2017; Marinelli & March, 1996; Marinelli et al., 1998, 2017; Porter & Melouk, 1997) and is caused by *Sclerotinia minor* and *S. sclerotiorum* (Marinelli & March, 1996; Porter & Melouk, 1997). These pathogens cause plant wilting, discoloration, stem necrosis, and death (Marinelli & March., 1996; Tariq et al., 1985; Willetts & Wong., 1980).

Strategies for the management of the disease, such as crop rotations, tillage practices, and fungicide applications, have remained inefficient (March et al., 2008; Smith et al., 2008; Vargas Gil et al., 2008). In recent years, the prevalence of Sclerotinia blight in Argentina has increased, reaching incidence scores of 50% (Oddino, 2015; Rosso et al., 2019). In this context, genetic resistance appears as one of the most important solutions in disease management. Although few peanut varieties with tolerance to *Sclerotinia* sp. (incidence values below 10%) have been developed in different parts of the world (Damicone et al., 2010; Partridge-Telenko et al., 2011), the only peanut variety in Argentina that shows tolerance (incidence) below 10% to *S. sclerotiorum* is the commercial high-oleic variety ''Pronto'' (Soave et al., 2008). The screening for genotypes with promising levels of resistance to Sclerotinia blight is the starting point for obtaining new resistant varieties.

The cultivated peanut presents a narrow genetic base; as reported by Moretzsohn et al. (2004), three factors or their combinations are the cause of low level of variation: (1) barriers to gene flow from related diploid species to domesticated peanut as a consequence of the polyploidization event; (2) recent polyploidization, from one or a few individual(s) of each diploid parental species, combined with self-pollination; or (3) use of few elite breeding lines and little exotic germplasm in breeding programs; thus, the wild species closely related to *A. hypogaea* constitute an important source of resistance to many pests and diseases (Stalker, 2017). Some of those resistances have been successfully transferred to commercial genotypes (de Blas et al., 2019; Pasupuleti et al., 2013; Simpson & Starr, 2001; Stalker, 2017; Stalker & Moss, 1987). Crosses with wild species allowed the selection of cultivated materials resistant to early leaf spot caused by *Cercospora arachidicola* S. Hori, late leaf spot caused by *Cercosporidium personatum* (Berk. and Curt.) Deighton (Moss et al., 1981; Stalker & Wynne., 1979; Wynne & Halward., 1989), Sclerotinia blight caused by *Sclerotinia minor* Jagger and *S. sclerotiorum* (Lib.) de Bary (Isleib et al., 2006; Tallury, Hollowell, et al., 2014), root-knot nematodes caused by *Meloidogyne arenaria* (Neal) (Ballén et al., 2019; Simpson & Starr, 2001), and peanut smut caused by *Thecaphora frezii* (de Blas et al., 2019, 2021).

**Core Ideas**

- Two genome regions that confer resistance to Sclerotinia blight were identified.
- Two consistent QTLs *qSbIA04* and *qSbIB04* were identified; they were located on chromosomes A04 and B04, respectively.
- From total phenotypic variance, the QTL *qSbIA04* explained 29%.
- From total phenotypic variance, the QTL *qSbIB04* explained 22%.

Since early 2000s molecular markers have been used on genetic improvement in peanuts (Ballén, 2019; Bertioli et al., 2014; Chu et al., 2019; Pandey et al., 2014; Varshney, 2016; Varshney et al., 2006). Single nucleotide polymorphisms (SNPs) are the most abundant DNA sequence variation in genomes and can be used as molecular markers to associate loci in the genome with phenotypic traits. Using these markers, Liang et al. (2020) reported quantitative trait loci (QTLs) associated with Sclerotinia blight resistance; Pandey et al. (2017) and Chu et al. (2019) for early, late leaf spot and tomato spotted wilt virus resistance; Varshney et al. (2014) for rust resistance, and de Blas et al. (2021) and Massa et al. (2021) for peanut smut.

The objective of the present study was to detect QTL associated with genetic resistance to *Sclerotinia minor* in the F8:10 recombined inbred line (RIL) mapping population derived from a cross between *A. hypogaea* and a synthetic amphidiploid [(*A. correntina* × *A. cardenasii*) × *A. batizocoi*] $^{4\times}$ (de Blas et al., 2019) to ultimately accelerate the genetic improvement process of Sclerotinia blight resistant peanut varieties.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant material

This study analyzed 103 individuals of an advanced RIL Sclerotinia blight segregant population (de Blas et al., 2019, 2021). Seeds of F8:10 generation were obtained by single seed descent from the F2 of a cross between a resistant

artificial amphidiploid JS 1806 (male) (Bima et al., 2011) and the susceptible experimental line *Arachis hypogaea* high-oleic JS 17304-7-B (female). The synthetic amphidiploid derives from cross between diploid wild *Arachis* species *A. cardenasii* (Krapov. & W.C. Greg (KSSc 36,015)) × *A. correntina* ((Burkart) Krapov. & W.C. Greg (K 11905)) × *A. batizocoi* (Krapov. & W.C. Greg (K 9484)) with subsequent duplication of chromosomes.

Seeds of the *A. hypogaea* experimental elite line JS 17304-7-B and amphidiploid JS 1806 were provided by Criadero El Carmen S.A. nursery, Argentina. All field assays were conducted in accordance with local legislation (Law No. 9164, Decree 132/05).

## 2.2 | Sclerotinia blight resistance evaluation

Phenotypic evaluation was done during the three growing seasons 2017/18, 2018/19, and 2019/20. All experiments were sown during the first week of December at Criadero El Carmen S.A. nursery, located in General Cabrera, Córdoba, Argentina (32°49′40′′S 63°52′14′′W). The experimental design consisted of 103 genotypes arranged in a randomized complete block with three replications. Each plot (genotype) consisted of 25 plants, evenly spaced in a 2.5 m row.

The rows were inoculated with mycelium and sclerotia of *Sclerotinia minor* a black and amorphous resistance structure approximately 0.5–3 mm in size. Inoculum was prepared by growing *S. minor* in glucose potato broth at 25°C for two weeks according to Rosso et al. (2021).

The inoculum was scattered at 90 and 120 DAS (days after sowing) and the disease progression was evaluated by recording the incidence in the field. All plants in the row were scored, estimating the degree of the infection at the beginning of the first symptoms, and at 30, 45, and 60 days after inoculation. Incidence was calculated as the ratio of the number of affected plants to the total number of plants in the row. Identification of an infected plant was based on disease symptoms, as well as signs such as spongy white mycelium and/or the presence of sclerotia.

## 2.3 | Statistical analysis

The Sclerotinia blight incidence datasets for the 103 RILs and parental lines were analyzed using a general and mixed linear model. The model included genotype, year, time of evaluation, and experimental unit where year, time, and genotype were taken as fixed effects and experimental unit as random effect. Mean comparison was done using the Di Rienzo, Guzmán and Casanoves (DGC) test (Di Rienzo et al., 2017). A general mixed model was fitted using *lme4* R package to calculate the broad-sense heritability for Sclerotinia blight resistance from variance components using the following equation:

$$H^2 = \sigma_g^2/(\sigma_e^2 + \sigma_g^2)$$

where $\sigma^2_g$ is the genotypic variance and $\sigma^2_e$ is the error variance.

A priori association analysis between disease resistance and SNP markers was done by single linear regression with 1819 SNP markers as the independent variable, and incidence as the dependent variable, using False Discovery Rate for multiple testing correction. SNPs with $p < 0.01$ were considered significantly associated with the trait.

## 2.4 | QTL analysis

The QTL mapping was carried out with the *R/qtl2* package using the genetic map constructed from the same population of RILs (de Blas et al., 2021). The adjusted means of the phenotypic data (incidence) of the 103 RILs obtained from the model described in statistical analysis, were used for QTL analysis. Haley–Knott (H-K) regression method was used to evaluate the association of each genome position with the trait of interest. The threshold log odds (LOD) score was estimated empirically using 1000 permutations ($p = 0.01$). A QTL was declared if the LOD score was above the empirical threshold. The percentage of phenotypic variation explained (PVE) for each QTL was calculated with the following equation:

$$PVE = (1 - \left(10^{\frac{-2*LOD}{N}}\right)) * 100$$

where $N$ is the number of individuals.

The QTLs were named according to conventional nomenclature with the initial letter "q" followed by the character name (here called Sclerotinia blight incidence (SbI)) and the linkage group (LG).

The approximate physical positions of the QTLs were defined by the closest genetic markers. The function *fitqtl* as implemented in *R/qtl* (Broman et al., 2003) by fitting a single linear model with each detected QTL, and the percentage of reduction of blight incidence was calculated by the differences in the percentage of incidence between genotypic classes at QTL positions. In addition, two-QTL scans were performed to assess loci interactions.

## 2.5 | Prospection of candidate genes within QTL intervals

To identify candidate genes that potentially regulate disease resistance against pathogenic fungi, genetic models were

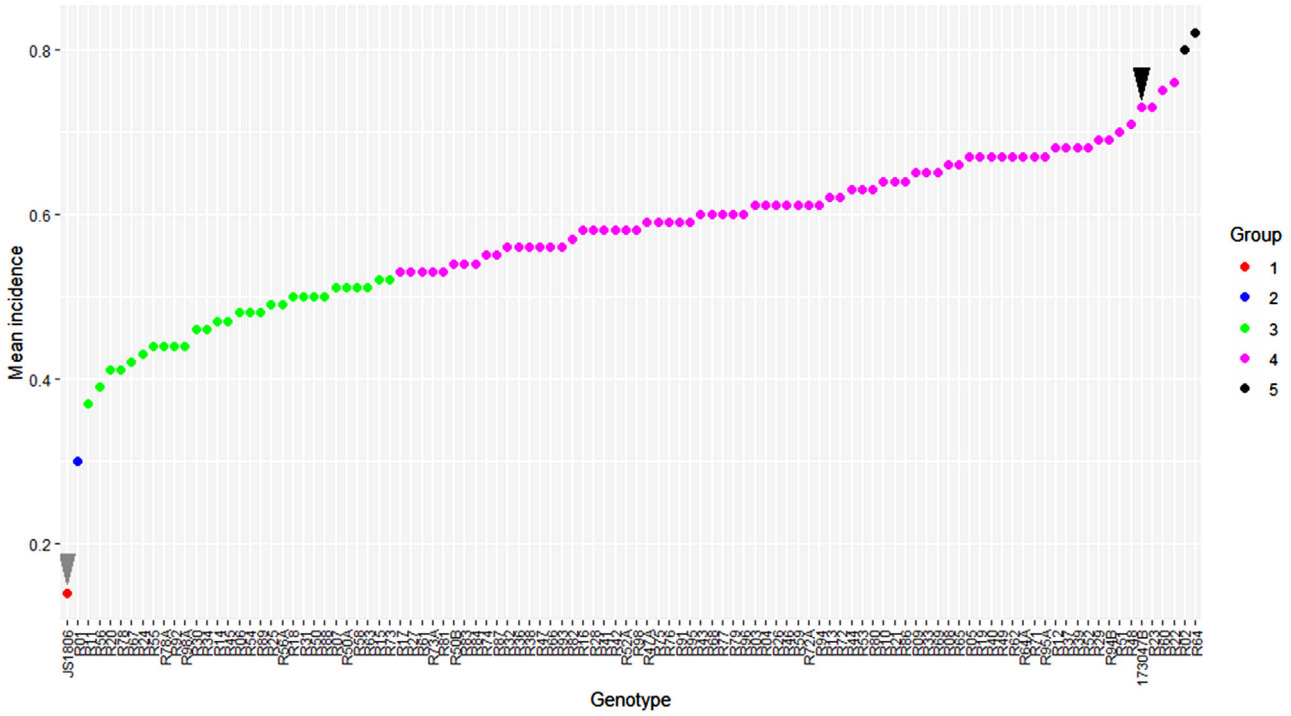


**FIGURE 1** Sclerotinia blight incidence values of 103 RILs derived from the cross between *A. hypogaea* JS 17304-7-B and the amphidiploid JS 1806. Susceptible and resistant parents are indicated with arrows in black and gray, respectively.

retrieved using the online platform https://mines.legumeinfo.org/peanutmine/begin.do. The QTL intervals were defined between the physical positions of the markers identified at the extremes of the confidence interval using the *lod_int* function in *R/qtl2* package. The physical positions were designated according to the reference sequence of *A. hypogaea* (Bertioli et al., 2019).

## 3 | RESULTS

### 3.1 | Disease evaluation

Statistically significant differences ($p = 0.05$) were found in disease incidence values between genotypes. For the susceptible parent JS 17304-7-B, the adjusted mean incidence of Sclerotinia blight was 0.73, while for the amphidiploid SJ 1806, the incidence was 0.14. A wide range of disease resistance was observed in the RILs. The DGC test grouped the RILs into five clusters (Figure 1). The synthetic amphidiploid presented the lowest value of incidence (0.14), followed by RIL R1 with 0.33 and 29 lines showing intermediate incidence values between 0.37 and 0.52. The other group consisted of 70 lines with incidence scores between 0.53 and 0.76 and did not show significant differences to the susceptible parental line JS 17304-7-B. Finally, transgressive segregation was observed in two RILs (R2, R64) presenting an incidence greater than 0.76, being more susceptible than cultivated parent. The broad-sense heritability calculated for this population was 0.16.

The record of incidence values in the susceptible and resistant genotypes during the three years confirm the success of the inoculation method and highlighted the high degree of resistance present in several genotypes.

### 3.2 | QTL analysis

After performing a single marker analysis to detect SNPs associated with SbI, 332 SNPs were found statistically significant ($p < 0.01$) in LGs A03, A04, A10, B01, B03, B04, and B10 (supplementary additional file S1).

The QTL analysis retrieved SNPs significantly associated with Sclerotinia blight disease incidence on chromosomes A03, A04, B01, B03, and B04, with LOD scores above the empirical threshold in two out of three years of disease evaluation. However, only two large-effect QTLs (Figure 2a) were detected for Sclerotinia blight resistance throughout three years of phenotypic evaluation with LOD scores above the empirical threshold at $p = 0.01$ (Figure 2b). The QTL *qSbIA04* was detected on chromosome A04 at 56.39 cM. The closest markers to the QTL peak (2.52 Mbp) were AX-176807568 and AX-176795814, and they showed a PVE of 29%. The QTL *qSbIB04* was found in chromosome B04 at

**TABLE 1** QTLs for resistance to Sclerotinia blight according to the QTL detection model of the Halley–Knott genome scan

| LG[a] | Genetic position (cM)[b] | Physical position (bp)[c] | SNP marker | LOD[d] | LOD threshold[e] | LOD interval[f] | PVE (%)[g] |
|---|---|---|---|---|---|---|---|
| A04 | 56.39 | 20291754 | AX-176807568 | 7.64 | 2.52 | 54.70-70.01 | 29 |
| | | 14466763 | AX-176795814 | | | | |
| B04 | 13.38 | 57856753 | AX-176812142 | 5.53 | 2.07 | 8.16-27.53 | 22 |

[a]Linkage group.
[b]Genetic position in cM for each LG.
[c]Physical position based on pseudomolecules of *A. hypogaea*.
[d]LOD score at QTL peak.
[e]LOD threshold based on 1000 permutations with a significance level of 1%.
[f]LOD interval.
[g]Proportion of the phenotypic variance explained by the QTL.

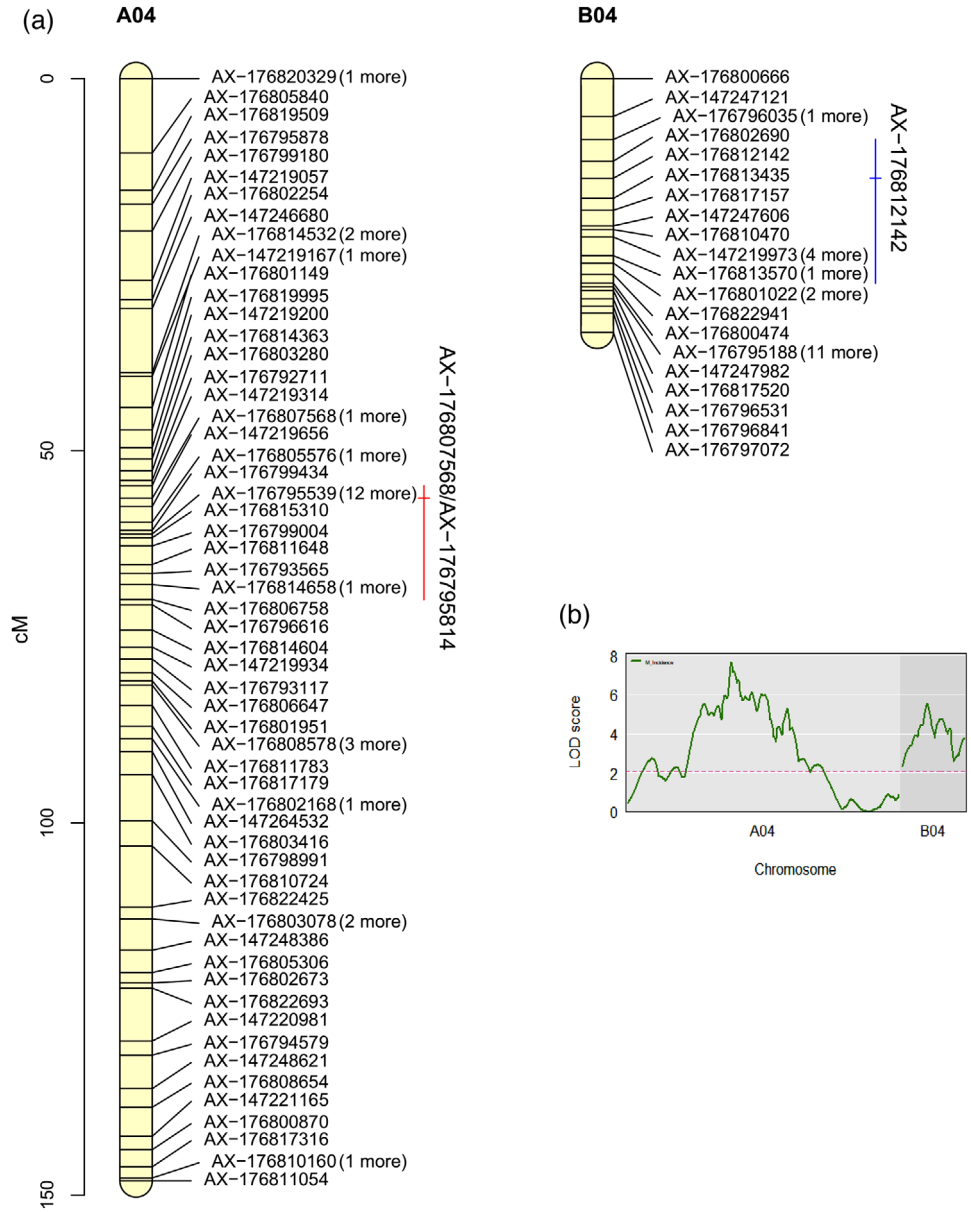


**FIGURE 2** QTLs for Sclerotinia blight resistance. (a): Detail of the A04 and B04 LGs showing the QTLs between LOD intervals as vertical bars and the peak as a horizontal dash. Y-axis indicates the genetic distance. Marker names (probesets 48 K ''Axiom_Arachis2'' SNP array) are indicated on the right of each LGs. (b): LOD scores per LGs A04 and B04; red dashed horizontal line indicates the empirical LOD score threshold at $p$-value < 0.01

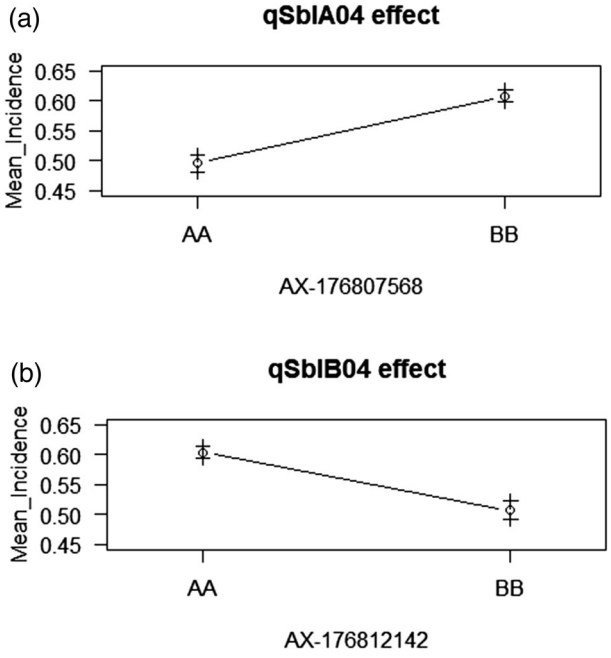


**FIGURE 3** Phenotypic effects of markers tightly linked to QTLs contributing to Sclerotinia blight resistance. (a): effect of genotype at AX-176807568. (b): effect of genotype at AX-176812142. AA and BB correspond to the amphidiploid and the peanut elite line genotypes, respectively.

13.38 cM. The closest marker to the QTL peak (2.07 Mbp) was AX-176812142, which showed a PVE of 22% (Table 1).

Among individuals with low mean incidence scores, alleles introgressed from wild and cultivated peanuts were detected. For *qSbIA04* the mean incidence decreased by 11% when the alleles came from wild peanuts, while for *qSbIB04* the mean incidence decreased by 10% when the alleles came from *A. hypogaea*. The statistically significant decrease in incidence for individual QTLs is shown in Figure 3. No interaction was detected between the two QTLs and no statistically significant reduction in incidence was observed when QTLs were analyzed together.

### 3.3 | Prospection of candidate gene identification for Sclerotinia blight resistance

Candidate gene identification analysis retrieved 134 genes within chromosome A04 (*qSbIA04)* interval (14466763 to 20291754 bp), of which nine had potential disease resistance function (6.71%). On the other hand, seven genes within chromosome B04 (*qSbIB04)* interval (57000000 to 58000000 bp) were found; three of them have potential disease resistance function (42.8%). Among these genes, the disease-resistance response proteins and MLO (Mildew Locus O) stand out. The complete gene list is presented in supplementary additional file S2.

## 4 | DISCUSSION

### 4.1 | Disease evaluation

Reliable phenotypic evaluation remains the key to success in any genetic improvement program. The evaluation of two parental lines and their 103 derived RILs under high inoculum pressure resulted in the detection of RILs with low incidence and stable responses to the disease during three consecutive growing seasons. The phenotypic variability observed among the seasons evaluated may be explained as variation in the experimental conditions as these experiments were done under field conditions without a completely controlled environment. Therefore, differences in temperature, humidity, and rainfall may have influenced plant growth, disease establishment, and progress. Nevertheless, the genotypes with extreme disease response were consistent throughout the seasons, that is, the parental line SJ 1806 together with R1, R11, and R56 presented the lowest incidence values, while the parental line JS 17304-7-B together with R2 and R64 showed susceptibility to the disease over the years.

### 4.2 | QTL analysis

Two major QTLs associated with Sclerotinia blight resistance were detected in this study. One QTL was on chromosome A04 and the other was on B04 (*qSbIA04* and *qSbIB04)*, and both had high LOD scores. The single linear regression in which 332 SNPs were found statistically significant associated ($p < 0.01$), reinforces the results for QTL detection as long as the markers within the *qSbIA04* and *qSbIB04* intervals were the ones explaining the highest phenotypic variance. In our study, the broad-sense heritability (0.16), the number of classes defined by the DGC clustering (5), and the number of QTL detected as significant on chromosomes A03, A04, B01, B03, and B04 suggest quantitative-resistance genetic control. Nevertheless, we followed a conservative approach considering only two large-effect QTLs (Figure 2a), on chromosomes A04 and B04 detected for Sclerotinia blight resistance throughout three years of phenotypic evaluation for further discussion. The markers within these two major QTLs could be used as functional SNP markers in marker-assisted selection for new peanut Sclerotinia blight resistance.

The QTL analysis showed that resistance to Sclerotinia blight was introgressed from both parents, the wild and the cultivated. Previous surveys reported that wild species such as *A. correntina* and *A. cardenasii* are resistant to multiple diseases (Bertioli et al., 2021, 2021; de Blas et al., 2019; Tallury, Isleib, et al., 2014). In this work, we demonstrated the successful transference of the existing resistance in wild species (*A. correntina, A. cardenasii*, and *A. batizocoi*) into the population under study.

The introgression of resistance from susceptible progenitors has been reported in several QTL studies in different crops (Bernier et al., 2007; Bonamico et al., 2012; Liang et al., 2020). Liang et al. (2020) released the first QTL analysis study for Sclerotinia blight caused by *Sclerotinia minor* spp. in a peanut RIL population. They detected a total of eight QTLs, but with differences across years. Two of the QTLs reported by Liang et al. (2020) were located on chromosomes A04 and B04 in concordance with our work. Those chromosomes appear to play a central role in the resistance. The results obtained by Liang et al. (2020) are consistent with our findings, both groups of QTL are located on the same chromosomes, but in different segments. In this study, PVE values of 29% and 22% were higher than those obtained by Liang et al. (2020) (6.6-25.6%). The QTL qS14 reported by Liang et al. (2020) was also derived from the susceptible relative. The combination of genomes from divergent progenitors may create a different genetic background for the cultivated progenitor's genes on the B04 QTL interval that proved to be responsible for the resistance to the individuals bearing the cultivated parent's loci. Based on unpublished data from our group we have validated using the competitive allele PCR technique that the allele providing resistance comes from the *A. hypogaea* progenitor. The genetic architecture of the susceptible progenitor providing resistance after performing a divergent cross needs further study to fully understand this fact.

### 4.3 | Prospection of candidate genes for resistance to Sclerotinia blight

There are few studies reporting genes or QTLs associated with resistance to Sclerotinia blight development (Chenault et al., 2009; Liang et al., 2020; Livingstone et al., 2005). The gene analysis content within *qSbIA04* and *qSbIB04* intervals retrieved the MLO-like protein 12-like defense response (GO: 0006952); integral component of membrane (GO: 0016021), and the response of the disease-resistance protein to biotic stimulus (GO: 0009607); defense response (GO: 0006952). These families of genes have been studied in several crops, but the role that these gene families play in the resistance to *Sclerotinia minor* should be further investigated.

## 5 | CONCLUSIONS

Two major QTLs, associated with resistance to *Sclerotinia minor*, were identified in the studied RIL population. These genomic regions that control the resistance to this disease and associated markers will have application in molecular breeding for the development of peanut varieties with resistance to Sclerotinia blight, shortening times and improving the efficiency of selection of segregating genotypes with the desired attributes.

## AUTHOR CONTRIBUTIONS

**Melina H. Rosso**: Conceptualization, Formal analysis, Methodology, Supervision, Writing-original draft, Writing-review & editing; **Francisco J. de Blas**: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review & editing; **Alicia N. Massa**: Data curation, Investigation, Writing-review & editing; **Claudio Oddino**: Investigation; Damian F. Giordano: Methodology; **Jose G. Seijo**: Formal analysis, Writing-review & editing; **Renee S. Arias**: Resources; **Juan H. Soave**: Resources; **Sara J. Soave**: Resources; **Mario I. Buteler**: Conceptualization, Investigation; **Marina Bressano**: Conceptualization, Investigation, Methodology, Supervision, Writing-original draft, Writing-review & editing

## ACKNOWLEDGMENTS

This work was funded by Criadero El Carmen (Nursery El Carmen), CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Universidad Nacional de Córdoba (Facultad de Ciencias Agropecuarias), and USDA-Agricultural Research Service. This study was carried out within the Specific Agreement of Cooperation and Technical Assistance between Facultad de Ciencias Agropecuarias National University of Córdoba (UNC) and "El Carmen S.A." EX-2020-00122590-UNC-ME#FCA.

## ORCID

*Melina H. Rosso* https://orcid.org/0000-0003-4252-0023
*Francisco J. de Blas* https://orcid.org/0000-0003-4500-3072
*Jose G. Seijo* https://orcid.org/0000-0001-8699-2044

## REFERENCES

Ballén-Taborda, C., Chu, Y., Ozias-Akins, P., Timper, P., Holbrook, C. C., Jackson, S. A., Bertioli, D. J., & Leal-Bertioli, S. C. M. (2019). A new source of root-knot nematode resistance from *Arachis stenosperma* incorporated into allotetraploid peanut (*Arachis hypogaea*). *Scientific Report*, *9*, 17702. https://doi.org/10.1038/s41598-019-54183-1

Bernier, J., Kumar, A., Ramaiah, V., Spaner, D., & Atlin, G. (2007). A large effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Science*, *47*(2), 507–516. https://doi.org/10.2135/CROPSCI2006.07.0495

Bertioli, D. J., Clevenger, J., Godoy, I. J., Stalker, H. T., Wood, S., Santos, J. F., & Leal-Bertioli, S. C. (2021). Legacy genetics of *Arachis cardenasii* in the peanut crop shows the profound benefits of international seed exchange. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(38), 2104899118.

Bertioli, D. J., Jenkins, J., Clevenger, J., Dudchenko, O., Gao, D., Seijo, G., Leal-Bertioli, S. C. M., Ren, L., Farmer, A. D., Pandey, M. K., Samoluk, S. S., Abernathy, B., Agarwal, G., Ballén-Taborda, C., Cameron, C., Cambpell, J., Chavarro, C., Chitikineni, A., Chu, Y.,

& Schmutz, J. (2019). The genome sequence of segmental allotetraploid peanut *Arachis hypogaea*. *Nature Genetics*, *51*(5), 877–884. https://doi.org/10.1038/s41588-019-0405-z

Bertioli, D. J., Ozias-Akins, P., Chu, Y., Dantas, K. M., Santos, S. P., Gouvea, E., Guimarães, P. M., Leal-Bertioli, S. C. M., Knapp, S. J., & Moretzsohn, M. C. (2014). The use of SNP markers for linkage mapping in diploid and tetraploid peanuts. *G3 Genes|Genomes|Genetics*, *4*(1), 89–96. https://doi.org/10.1534/G3.113.007617

Bima, P. J., Turina, C., Martino, C., Bracamonte, M., Ordóñez, A., Buteler, M., & Soave, J. (2011). In vitro production of synthetic amphidiploids from interspecific hybrids of the genus *Arachis* (In Spanish). *XXVI jornada nacional del maní*. (pp. 1–3), General Cabrera, Córdoba, Argentina.

Bonamico, N. C., di Renzo, M. A., Ibañez, M. A., Borghi, M. L., Díaz, D. G., Salerno, J. C., & Balzarini, M. G. (2012). QTL analysis of resistance to Mal de Río Cuarto disease in maize using recombinant inbred lines. *The Journal of Agricultural Science*, *150*(5), 619–629. https://doi.org/10.1017/S0021859611000943

Broman, K. W., Wu, H., Saunak, S., & Churchill, G. A. (2003). R/qtl: QTL mapping in experimental crosses. *Bioinformatics*, *19*(7), 889–890. https://doi.org/10.1093/bioinformatics/btg112

Chenault, K. D., Maas, A. L., Damicone, J. P., Payton, M. E., & Melouk, H. A. (2009). Discovery and characterization of a molecular marker for *Sclerotinia minor* (Jagger) resistance in peanut. *Euphytica*, *166*(3), 357–365. https://doi.org/10.1007/s10681-008-9816-0

Chu, Y., Chee, P., Culbreath, A., Isleib, T. G., Holbrook, C. C., & Ozias-Akins, P. (2019). Major QTLs for resistance to early and late leaf spot diseases are identified on chromosomes 3 and 5 in peanut (*Arachis hypogaea*). *Frontiers in Plant Science*, *10*, 883. https://doi.org/10.3389/FPLS.2019.00883

Damicone, J. P., Holbrook, C. C., Smith, D. L., Melouk, H. A., & Chamberlin, K. D. (2010). Reaction of the core collection of peanut germplasm to Sclerotinia blight and pepper spot1. *Peanut Science*, *37*(1), 1–11. https://doi.org/10.3146/PS09-001.1

de Blas, F. J., Bressano, M., Teich, I., Balzarini, M. G., Arias, R. S., Manifesto, M. M., Costero, B. P., Oddino, C., Soave, S. J., Soave, J. A., Buteler, M. I., Massa, A. N., & Seijo, J. G. (2019). Identification of smut resistance in wild *Arachis* species and its introgression into peanut elite lines. *Crop Science*, *59*(4), 1657–1665. https://doi.org/10.2135/CROPSCI2018.10.0656

de Blas, F. J., Bruno, C. I., Arias, R. S., Ballén-Taborda, C., Mamani, E., Oddino, C., Rosso, M., Costero, B. P., Bressano, M., Soave, J. H., Soave, S. J., Buteler, M. I., Seijo, J. G., & Massa, A. N. (2021). Genetic mapping and QTL analysis for peanut smut resistance. *BMC Plant Biology*, *21*(1), 1–15. https://doi.org/10.1186/S12870-021-03023-4/TABLES/3

Di Rienzo, J. A., Casanoves, F., Balzarini, M. G., Gonzalez, L., Tablada, M., & Robledo, C. W., INFOSTAT (2017). *Grupo Infostat*. FCA, Universidad Nacional de Córdoba, Argentina. http://www.infostat.com.ar

FAOSTAT. (2019). *Statistical database FAOSTAT*. Food and Agriculture Organization of the United Nations. http://faostat3.fao.org

Faske, T. R., Drennan, G., & Hurd, K. (2017). First report of Sclerotinia blight caused by *Sclerotinia sclerotiorum* on peanut in Arkansas. *Plant Health Progress*, *18*(1), 7–8.

Isleib, T. G., Rice, P. W., Mozingo, R. W., Copeland, S. C., Graeber, J. B., Shew, B. B., Smith, D. L., Melouk, H. A., & Stalker, H. T. (2006). Registration of N96076L peanut germplasm line. *Crop Science*, *46*(5), 2329–2330. https://doi.org/10.2135/CROPSCI2005.12.0479

Isleib, T. G., & Wynne, J. C. (1992). Use of plant introductions in cultivar development part 2. *Crop Science*, *20*, 77–116. https://doi.org/10.2135/CSSASPECPUB20

Liang, Y., Cason, J. M., Baring, M. R., & Septiningsih, E. M. (2020). Identification of QTLs associated with Sclerotinia blight resistance in peanut (*Arachis hypogaea* L.). *Genetic Resources and Crop Evolution*, *68*, 629–637. https://doi.org/10.1007/s10722-020-01012-4

Livingstone, D. M., Hampton, J. L., Phipps, P. M., & Grabau, E. A. (2005). Enhancing resistance to *Sclerotinia minor* in peanut by expressing a barley oxalate oxidase gene. *Plant physiology*, *137*(4), 1354–1362. https://doi.org/10.1104/pp.104.057232

March, G. J., Vargas Gil, S., Marinelli, A. D., Oddino, C., & Zuza, M. (2008). Diseases caused by soil fungi in peanut—Management strategies (In Spanish). IDIA XXI–Cultivos industriales (pp. 42–45).

Marinelli, A. D., & March, G. J. (1996). Epidemics of Sclerotinia blight (*Arachis hypogaea* L.) caused by *Sclerotinia sclerotiorum* (Lib.) of bary and *S. minor* Jagger in Argentina (In Spanish). *Boletín de Sanidad Vegetal*, *22*(3), 501–510.

Marinelli, A. D., March, G. J., & Oddino, C. M (2017). Peanut fungal diseases. (In Spanish). In E. Fernandez, & O. Giayetto (Eds.), *Peanut crop in Argentina* (2nd ed., pp. 385–311). Las Higueras.

Marinelli, A. D., March, G. J., Rago, A., & Giuggia, J. (1998). Assessment of crop loss in peanut caused by *Sclerotinia sclerotiorum, S. minor*, and *Sclerotium rolfsii* in Argentina. *International Journal of Pest Management*, *44*(4), 251–254. https://doi.org/10.1080/096708798228185

Massa, A. N., Bressano, M., Soave, J. H., Buteler, M. I., Seijo, G., Sobolev, V. S., Orner, V. A., Oddino, C., Soave, S. J., Faustinelli, P. C., de Blas, F. J., Lamb, M. C., & Arias, R. S. (2021). Genotyping tools and resources to assess peanut germplasm: Smut-resistant landraces as a case study. *PeerJ*, *9*, e10581. https://doi.org/10.7717/peerj.10581

Moretzsohn, M. d. C., Hopkins, M. S., Mitchell, S. E., Kresovich, S., Francisco, J., Valls, M., Ferreira, M. E., & Genéticos, E. R. (2004). Genetic diversity of peanut (*Arachis hypogaea* L.) and its wild relatives based on the analysis of hypervariable regions of the genome. *BMC Plant Biology*, *4*. https://doi.org/10.1186/1471-2229-4-11

Moss, J. P., Spielman, V., Burge, A. P., Singh, A. K., & Gibbons, R. W. (1981). Utilization of wild *Arachis* species as a source of Cercospora leaf spot resistance in groundnut breeding. In G. K. Marna, & U. Sinha (Eds.), *Perspectives in cytology and genetics*. (pp. 673–677) Hindasia Publishing. https://doi.org/10.1007/BF00021154

Oddino, C. (2015). Soil pathogen diseases in peanuts. *Dissertation. XXX jornada nacional del maní*. General Cabrera, Córdoba.

Pandey, M. K., Wang, H., Khera, P., Vishwakarma, M. K., Kale, S. M., Culbreath, A. K., Holbrook, C. C., Wang, X., Varshney, R. K., & Guo, B. (2017). Genetic dissection of novel QTLs for resistance to leaf spots and tomato spotted wilt virus in peanut (*Arachis hypogaea* L.). *Frontiers in Plant Science*, *8*, 25. https://doi.org/10.3389/FPLS.2017.00025/BIBTEX

Pandey, M. K., Wang, M. L., Qiao, L., Feng, S., Khera, P., Wang, H., Tonnis, B., Barkley, N. A., Wang, J., Holbrook, C. C., Culbreath, A. K., Varshney, R. K., & Guo, B. (2014). Identification of QTLs associated with oil content and mapping *FAD2* genes and their relative contribution to oil quality in peanut (*Arachis hypogaea* L.). *BMC Genetics*, *15*, 133. https://doi.org/10.1186/s12863-014-0133-4

Partridge-Telenko, D. E., Hu, J., Livingstone, D. M., Shew, B. B., Phipps, P. M., & Grabau, E. A. (2011). Sclerotinia blight resistance in Virginia-type peanut transformed with a barley oxalate oxidase gene.

*Phytopathology*, *101*(7), 786–793. https://doi.org/10.1094/PHYTO-10-10-0266

Pasupuleti, J., Nigam, S. N., Pandey, M. K., Nagesh, P., & Varshney, R. K. (2013). Groundnut improvement: Use of genetic and genomic tools. *Frontiers in Plant Science*, *4*, 23. https://doi.org/10.3389/FPLS.2013.00023

Porter, D. M., & Melouk, H. A. (1997). Sclerotinia blight. In N. Kokalis-Burelle, D. M. Porter, R. Rodriguez-Kabana, D. H. Smith, & P. Subrahmanyam (Eds.), *Compendium of peanut diseases* (2nd ed., pp. 34–36). The American Phytopathological Society.

Porter, D. M., Smith, D. H., & Rodriguez-kabana, R. (1982). *Peanut disease. Peanut science and technology* (pp. 348–378) American Peanut Research and Education Society.

Rosso, M., Bressano, M., de Blas, F., Oddino, C., Soave, S., Giordano, D. F., & Soave, J. (2021). Development and validation of a field inoculation technique for *Sclerotinia minor* in peanut crops. (In Spanish, with English abstract). *AgriScientia*, *38*(2), 127–133. https://doi.org/10.31047/1668.298x.v38.n2.31060

Rosso, M., Soave, S., Soave, J., de Blas, F., Bressano, M., Giordano, F., Giuggia, J., Garnero, J. M., Seijo, G., Moresi, A., Buteler, M., & Oddino, C. (2019). Characterization of the germplasm of Criadero El Carmen against Sclerotinia blight caused by *Sclerotinia minor*. (In Spanish). *Summaries XXXIV jornada nacional del maní*. (pp. 38–39). General Cabrera, Córdoba.

SAGPyA- Secretaria de Agricultura, Ganadería, Pesca y Alimentos. (2020). https://www.magyp.gob.ar/sitio/areas/ss_mercados_agropecuarios/apertura_de_mercados/analisis_foda/index.php.

Simpson, C. E., & Starr, J. L. (2001). Registration of "COAN" peanut. *Crop Science*, *41*(3), 918–918. https://doi.org/10.2135/cropsci2001.413918x

Smith, D. L., Garrison, M. C., Hollowell, J. E., Isleib, T. G., & Shew, B. B. (2008). Evaluation of application timing and efficacy of the fungicides fluazinam and boscalid for control of Sclerotinia blight of peanut. *Crop Protection*, *27*(3–5), 823–833. https://doi.org/10.1016/J.CROPRO.2007.11.010

Soave, J., Oddino, C., Bianco, C., Soave, S., Moresi, A., & Buteler, M. (2008). "Pronto (AO)": New short-cycle and high oleic peanut variety tolerant to Sclerotinia blight caused by Sclerotinia sclerotiorum (In Spanish). *XXIII Jornada Nacional Del Maní y 1o Simposio de Maní Del Mercosur*., General Cabrera, Córdoba.

Stalker, H. T. (2017). Utilizing wild species for peanut improvement. *Crop Science*, *57*(3), 1102–1120. https://doi.org/10.2135/CROPSCI2016.09.0824

Stalker, H. T., & Moss, J. P. (1987). Speciation, cytogenetics, and utilization of *Arachis* species. *Advances in Agronomy*, *41*(C), 1–40. https://doi.org/10.1016/S0065-2113(08)60801-9

Stalker, H. T., & Wynne, J. C. (1979). Cytology of interspecific hybrids in section *Arachis* of peanuts. *Peanut Science*, *6*, 110–114. https://doi.org/10.3146/i0095-3679-6-2-12

Tallury, S. P., Hollowell, J. E., Isleib, T. G., & Stalker, H. T. (2014). Greenhouse evaluation of section *Arachis* wild species for Sclerotinia blight and Cylindrocladium black rot resistance. *Peanut Science*, *41*(1), 17–24. https://doi.org/10.3146/PS13-02.1

Tallury, S. P., Isleib, T. G., Copeland, S. C., Rosas-Anderson, P., Balota, M., Singh, D., & Stalker, H. T. (2014). Registration of two multiple disease-resistant peanut germplasm lines derived from *Arachis cardenasii* krapov. & W.C. gregory, GKP 10017. *Journal of Plant Registrations*, *8*(1), 86–89. https://doi.org/10.3198/JPR2013.04.0017CRG

Tariq, V. - N., Gutteridge, C. S., & Jeffries, P. (1985). Comparative studies of cultural and biochemical characteristics used for distinguishing species within *Sclerotinia*. *Transactions of the British Mycological Society*, *84*(3), 381–397. https://doi.org/10.1016/S0007-1536(85)80001-2

Vargas Gil, S., Haro, R., Oddino, C., Kearney, M., Zuza, M., Marinelli, A., & March, G. J. (2008). Crop management practices in the control of peanut diseases caused by soilborne fungi. *Crop Protection*, *1*(27), 1–9. https://doi.org/10.1016/J.CROPRO.2007.03.010

Varshney, R. K. (2016). Exciting journey of 10 years from genomes to fields and markets: Some success stories of genomics-assisted breeding in chickpea, pigeon pea and groundnut. *Plant Science*, *242*, 98–107. https://doi.org/10.1016/J.PLANTSCI.2015.09.009

Varshney, R. K., Hoisington, D. A., & Tyagi, A. K. (2006). Advances in cereal genomics and applications in crop breeding. *Trends in Biotechnology*, *24*(11), 490–499. https://doi.org/10.1016/J.TIBTECH.2006.08.006

Varshney, R. K., Pandey, M. K., Pasupuleti, J., Shyam, N. N., Sudini, H., Gowda, M. V. C., Sriswathi, M., Radhakrishnan, T., Surendra, M. S., & Nagesh, P. (2014). Marker-assisted introgression of a QTL region to improve rust resistance in three elite and popular varieties of peanut (*Arachis hypogaea* l.). *Theoretical and Applied Genetics*, *127*, 1771–1781. https://doi.org/10.1007/s00122-014-2338-3

Willetts, H. J., & Wong, J. A. L. (1980). The biology of *Sclerotinia sclerotiorum, S. trifoliorum*, and *S. minor* with emphasis on specific nomenclature. *The Botanical Review*, *46*(2), 101–165. https://doi.org/10.1007/BF02860868

Wynne, J. C., & Halward, T. (1989). Cytogenetics and genetics of Arachis. *Critical Reviews in Plant Sciences*, *8*, 189–220. https://doi.org/10.1080/07352688909382275

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Rosso, M. H, de Blas, F. J, Massa, A. N, Oddino, C., Giordano, D. F., Seijo, J. G., Arias, R. S., Soave, J. H., Soave, S. J., Buteler, M. I., & Bressano, M. (2023). Two QTLs govern the resistance to *Sclerotinia minor* in an interspecific peanut RIL population. *Crop Science*, *63,* 613–621. https://doi.org/10.1002/csc2.20875