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Assessment of Resistance to Late Blight (*Phytophthora infestans* (Mont.) de Bary) in Chilean Native Potatoes (*Solanum tuberosum Chilotanum group*)

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Abstract

Phytophthora infestans (Mont.) de Bary is a highly destructive oomycete in potato crops, and managing its impact is crucial. Host plant resistance plays a pivotal role in disease management. This study aimed to evaluate the resistance to late blight in nine preselected Chilean native potato genotypes through field and laboratory experiments, comparing them with the moderately susceptible control cultivar Désirée. The field trial spanned two seasons (2017/2018 and 2018/2019) at the same location in Southern Chile. Foliar damage percentage caused by natural infection was measured, and the relative area under the disease progress curve (rAUDPC) was calculated. The laboratory experiments included a detached leaflet assay and a tuber assay in 2019. The results indicated that seven genotypes, Azul (0.10), SN-1 (0.10), Chilca-1 (0.11), Azul Casposa (0.07), Corahila Reina (0.16), Piku (0.17) and Murta (0.24), exhibited partial resistance with significantly lower rAUDPC values than the control cultivar across both seasons. Moreover, the detached leaflets assay in 2019 highlighted four genotypes with substantially lower damage percentages: Azul Casposa (0.11%), Chilca-1 (0.64%), Piku (1.11%) and SN-1 (3.16%). The tuber assay conducted in 2019 revealed that five of the foliar-resistant genotypes, Azul (43.98%), SN-1 (38.06%), Chilca-1 (41.54%), Corahila Reina (45.5%) and Murta (39.11%), exhibited low to medium resistance also in tubers. This study successfully identified favourable variation for *Phytophthora infestans* resistance, indicating the potential suitability of given Chilean native potato germplasm as donors in potato breeding programs.

Keywords Chilean native potatoes · Detached leaflet assay · Late blight · rAUDPC · Resistance · Tuber assay

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Introduction

The cultivated potato (*Solanum tuberosum* ssp. *tuberosum*) is the highest-producing tuber crop in the world (FAOSTAT 2023). Potatoes play an important role in developing countries' food security, as they, along with rice, wheat and maize, supply 50% of the world's food energy needs (Wijesinha-Bettoni and Mouillé 2019). Notably, the share of global potato output from developing countries now surpasses that of developed countries. In 2013, global potato consumption averaged 35 kg/capita/year, with significant regional differences (Wijesinha-Bettoni and Mouillé 2019). Thus, this crop plays a crucial role as a primary food source for millions of people worldwide, especially in regions where it serves as staple crop, providing essential nutrients and sustaining livelihoods.

The late blight disease caused by *Phytophthora infestans* is highly destructive in potato crops and was responsible for the Irish famine in 1845 (Powderly 2019). Globally, the annual yield loss and management costs for potato late blight can accumulate to 3–10 billion USD (Dong and Zhou 2022). In developing countries, late blight leads to losses exceeding 60% of the yield. Conversely, in developed countries, pesticide costs could represent 10 to 25% of the market value of the potato harvest (Dong and Zhou 2022). A simulation considering climate change and late blight indicated an increased risk of the disease between 1975 and 2050, particularly affecting susceptible varieties in Europe, Asia, Africa, North and South America (Sparks et al. 2014). Mancozeb, one of the most commonly used fungicides to control late blight in potatoes, has been banned for agricultural use by the European Union as of January 2022 due to its hazards to humans and the environment (Ben and Cohen 2023). According to Pacilly et al. (2016), current and future pesticide policies significantly restrict the use of fungicide, limiting the use of the most popular alternatives to control this plant disease. The EU resolution includes a goal of reducing the use of pesticides by 50% by 2030 (European Commission 2020). Among the integrated disease management practices for late blight, the effective use of resistant varieties allows for an efficient and sustainable control program (Acuña and Bravo 2019). For instance, under experimental conditions, varieties that have been cisgenically modified with stacked resistance genes allowed reductions of fungicide use by 80–90% to control late blight (Kessel et al. 2018), while a review indicated moderate reductions of 50–80% (Schneider et al. 2023).

Cultivation of late blight-resistant varieties is the most effective and environmentally friendly approach to control potato late blight disease (Duan et al. 2021). In organic potato production, there is an urgent need for varieties with durable late blight resistance developed through classical breeding programs (Keijzer et al. 2022). Additionally, among the opportunities and challenges in sustainable potato-based agri-food systems, there is an urgent need for the supply of locally adapted varieties that are tolerant or resistant to pests (Devaux et al. 2021).

Resistance conferred by *R* genes (*Rpi* genes) is the most effective non-chemical strategy against *P. infestans* infection. However, the scarcity of potato varieties with this resistance, combined with the rapid breakdown of *R* gene resistance

due to the virulence variability of *P. infestans*, continues the demand of fungicide use to control this disease (Elnahal et al. 2020; Paluchowska et al. 2022). Consequently, numerous efforts have been made to identify *Rpi* genes in a variety of potato populations, including both landraces and wild relatives, with the aim of transferring them to cultivated potato varieties (Paluchowska et al. 2022; Ordoñez et al. 2023). For instance, novel late blight resistance sourced from wild diploid accessions of series Tuberosa (*Solanum cajamarquense*) and Megistracroloba (*Solanum sogarandinum*) has been introgressed into tetraploid potato. These 4×hybrids are now used as donors in potato breeding programs (Ordoñez et al. 2023).

P. infestans has spread across the globe, and understanding the mechanisms of its repeated global emergence is critical (Goss et al. 2014). Recent studies have shown that the centre of origin for potato late blight is Central America (Goss et al. 2014; Martin et al. 2019), from where it has migrated to South and North America, Europe and beyond (Martin et al. 2014, 2016, 2019). This oomycete is a diploid heterothallic species, requiring the pairing of A1 and A2 mating types to produce long-lived sexual oospores (Martin et al. 2019). In Southern Chile, *P. infestans* populations are predominantly clonal, characterised by the A1 mating type (Sandoval et al. 2019). Up to 2005, the dominant genotype was US1; however, by 2016, the 2-A1 genotype became predominant. Furthermore, as of 2015, these populations showed the presence of 11 avirulence genes (avr1 to avr11) and three *P. infestans* variants (Sandoval et al. 2019). Notably, genes *avr1*, *avr3*, *avr5*, *avr7*, *avr8*, *avr10* and *avr11* were particularly prevalent, each found in over 90% of *P. infestans* isolates from 2014 to 2015 (Sandoval et al. 2019). Avr proteins, also known as effectors, encode a protein featuring a canonical RXLR motif (Anderson et al. 2015). They can be detected by nucleotide-binding domain leucine-rich repeat-containing (NLR) receptors, triggering effector-triggered immunity (ETI), a defensive response against pathogens (Ngou et al. 2022). Especially in wild potatoes, there are 12 *R* genes in response to several *avr* genes in *P. infestans* (Du and Vleeshouwers 2017). For instance, the R1 receptor in host plants detects the *P. infestans* Avr1 effector, prompting an ETI that culminates in a hypersensitive response and consequent resistance (Du et al. 2015b). Furthermore, other receptors, such as pattern recognition receptors (PRRs), may also play pivotal roles in establishing long-term resistance against late blight (Du et al. 2015a; Du and Vleeshouwers 2017).

South America is recognised as the origin centre of *S. tuberosum*, with Chile designated as a sub-center of origin (Jansky and Spooner 2018). The Potato Genebank at Universidad Austral de Chile (UACh; https://www.potatogenebank.cl/) houses 279 genotypes of native potatoes *S. tuberosum* ssp. *tuberosum*, *Chilotanum* group. These genotypes have undergone evaluations for several biotic resistances, including resistances to potato virus Y (PVY), potato virus X (PVX), *Globodera pallida* and *Globodera rostochiensis*, utilizing molecular markers (López et al. 2015). Additionally, these potatoes have been assessed for various phenotypic traits, such as anthocyanin content, which might contribute to pathogen defence (Solis et al. 2021; Behn et al. 2023). In a separate study, Solano et al. (2014) identified four native *S. tuberosum* genotypes from southern Chile that exhibited resistance to late blight.

Preliminary field screenings for late blight, focusing on the aerial parts of potato genotypes at UACh Potato Genebank, identified nine genotypes from the *Chilotanum* group with robust performance and retained green foliage, even in the presence of the oomycete pathogen. Consequently, this observation prompted our current study, aiming to assess *P. infestans* resistance in both leaves and tubers through field and laboratory assays considering the nine preselected native potatoes from the *Chilotanum* group.

Materials and Methods

Plant Material

Nine potato genotypes were chosen from the UACh Potato Genebank based on their resistance to late blight, as evaluated in preliminary field screenings. The genotypes indicated a score of 2, except for Murta, which scored 3. The selected genotypes were Azul Casposa, Azul, Chilca-1, Corahila Reina, Murta, Papa Oro, Piku, Rosada Ojuda and SN-1. The selection was carried out over two seasons using a scoring scale from 1 (resistant) to 9 (susceptible). The cultivar Désirée was used as a control, as it has been described as moderately susceptible to late blight in southern Chile, based on rAUDPC data (Solano et al. 2014). Conversely, in an assay conducted in Spain, Désirée was considered to be resistant according to rAUDPC (Meno et al. 2023). The European Cooperative Programme for Plant Genetic Resources (ECPGR) 2023 further reports that cv. Désirée shows medium resistance to late blight on foliage under field conditions. In laboratory tests, the cultivar presents low to medium resistance both on foliage and in tuber assessments (ECPGR 2023).

Field Experiment

The nine selected genotypes, along with the cv. Désirée, were evaluated over two seasons (2017/2018 and 2018/2019) in field trials at the Estación Experimental Agropecuaria Austral (EEAA, 39°47′ LS, 73°14′ W, 19 m a.s.l.) in the Los Rios Region, Chile. The local soil is a Duric Hapludand soil from the Valdivia series, with a bulk density of 0.7 g/cm^3 and an organic matter content of 15% (Ávila-Valdés et al. 2020). Agroclimatic data were taken from the Austral Valdivia meteorological station, located in the EEAA, approximately 500 m away from the potato field trial site.

Seed potatoes were taken from the working collection of the UACh Potato Genebank. Tubers with healthy skin and of similar size were chosen within each genotype for planting. Trials for the first season started on October 12, 2017, and on October 16, 2018, for the second season. The experimental unit was a row of 10 plants, spaced at 0.7 m between rows and 0.3 m apart within a row. Rows were randomised within blocks following a randomised block design with three repetitions for the first season and four for the second.

After planting, the crop was fertilised with a rate of 1200 kg/ha using an N/P/K ratio of 11:30:11 (COPEVAL Fertilizer Mixture), according to the reference

guidelines for a target potato yield of 40 tons/ha, considering the minimal available N/P/K in the soil (Sandaña 2014). Before plant emergence, weed control was accomplished through a single application of Metribuzin 480 SC with a dosage of 0.56 L/ha, following the manufacturer's instructions. This approach was aligned with the recommended weed control practices for potato cultivation in the south-central area of Chile (Sandaña and Valenzuela 2017). Manual weeding was performed as needed throughout the growth periods. Sixty days after planting, when the plants reached heights between 20 and 30 cm, they were hilled. Sprinkler irrigation was administered from mid-January until the end of the growing seasons.

Infection by *P. infestans* originated from natural field inoculum. The genotypes were subsequently evaluated using the late-blight rating system developed by the Cornell University Department of Plant Pathology and Plant–Microbe Biology (Fry Lab 2013), which was adapted for use in this study (Table S1). Evaluations started once initial disease symptoms were observed. Each experimental unit was screened three times each season. During the first season, these screenings occurred at 95, 105 and 110 DAP (days after planting). For the second season, they were conducted at 94, 107 and 114 DAP. Following this, the relative area under the disease progress curve (rAUDPC) was determined using equations referenced in the literature (Simko and Piepho 2012).

P. infestans Isolation and Inoculum

To isolate *P. infestans*, potato leaves with late blight infection were collected from the same location as the field experiment during the 2018/2019 period. Mycelium was directly extracted from these infected leaves and placed on sterilised Petri dishes containing rye B agar to induce sporulation (Caten and Jinks 1968). The culture was then maintained in a controlled environment chamber at 17 °C in the darkness for 2 weeks. *P. infestans* characterisation was carried out by morphologically observing lemon-shaped sporangia and coenocytic mycelium under a microscope. For inoculation, mycelium was removed from the Petri dishes, suspended in sterile distilled water, and the number of sporangia was counted using a Neubauer chamber without filtration. The concentration was adjusted to 5×10^5 sporangia per millilitre through dilution. The inoculum was then stored for 1 h at temperatures between 3 and 4 °C to facilitate zoospore differentiation and release (Laviola et al. 1978).

Detached Leaflet Assay

Healthy leaflets were collected at 98 DAP from the 2018/2019 field trial during the morning. For each sampling, a leaflet was sourced from 10 distinct plants. However, the genotypes Murta, Papa Oro and Rosada Ojuda were excluded from this study because they lacked healthy green leaves when the assay was conducted.

Upon collection, the leaflets were securely stored in polyethylene bags and transported in a cooler filled with ice to preserve their freshness. In the laboratory, each leaflet was cleaned using dish soap, disinfected in a 0.5% sodium hypochlorite

solution for 10 min, and subsequently rinsed with sterile water in a laminar flow chamber to ensure aseptic conditions.

For the inoculation procedure, 10 leaflets per genotype were treated on their abaxial surface with 50 µl of inoculum. Additionally, four control leaflets were treated with 50 µl of sterile distilled water. These treated leaflets were then placed in a humidity-controlled chamber. This chamber was set up using a disinfected plastic tray that had been treated with 70% ethanol and then exposed to ultraviolet light for 2 min. Sterile absorbent paper, dampened with 50 ml of sterile distilled water, was laid in the tray. The leaflets were covered with a transparent polythene bag to maintain a humid environment. These chambers were then incubated at 15 °C with a 16-h light photoperiod for 7 days. The entire experiment was conducted in four separate trays following a block design.

To evaluate leaflet resistance, photographs were taken using a Fujifilm FinePix SL camera against a white backdrop. The damaged area, healthy green region and the total area of each leaflet were quantified using ImageJ software (Reinking 2007), which facilitated the subsequent computation of the damage percentage.

Tuber Assay

Healthy tubers were taken from different plants the 2018/2019 field trial in April. In the laboratory, the tubers were washed, disinfected and rinsed using the same procedure as described for the leaflet assay. Each tuber was then pricked five to six times with a sterile needle to a depth of 5 mm on opposite sides on the middle of the tuber. Subsequently, five tubers were inoculated at that injured tissue with 50 µl of inoculum. Additionally, as a control, two tubers were inoculated with 50 µl of sterile distilled water. The treated tubers were placed in the humidity-controlled chamber previously described and incubated at 15 °C in complete darkness for 30 days. This experiment was repeated in three separate trays, following a block design.

For resistance quantification, each tuber was bisected, and the damaged area was measured using the procedure outlined in the detached leaflet assay. The genotype Rosada Ojuda was excluded from evaluation because its purple hue interfered with the distinction of the damaged regions.

Statistical Analysis

The statistical analyses were conducted using Statgraphics Centurion XV, and the graphics were created using GraphPad Prism Version 8.0.2 (263). An ANOVA was conducted to analyze the rAUDPC with the entire dataset from the first and second seasons using the following model:

$$P_{jk} = \mu + G_i + Y_j + (G \times E)_{ij} + B(E)_{jk} + R_{ijk}$$

where P_{jk} = rAUDPC, μ = general mean, G_i = genotype i, E_j = season effect j, $(G \times E)_{ij}$ = interaction between genotype i and season j, $B(Y)_{jk}$ = effect of block k nested in season j, R_{ijk} = residual effect.

For the detached leaflet assay and the tuber assay, the mean of each block was calculated (expressed as a percentage of damage), without individualizing the leaflets and tubers for the scoring. Subsequently, the data mean per block underwent an arcsine transformation. Then, an ANOVA was carried out to analyze the damage percentage using the following model:

$$D_{ij} = \mu + G_i + B_j + R_{ij}$$

where D_{ij} = Arcsine damage percentage, μ = general mean, G_i = genotype i, B_j = block effect j, and R_{ij} = residual effect.

The Fisher's least significant difference (LSD) test was utilised to compare the mean of cv. Désirée with the mean of the genotypes, using a significance level of 5%. The means obtained from the field trials, detached leaflet ANOVA and tuber ANOVA were correlated using Pearson's correlation test in GraphPad Prism Version 8.0.2 (263) software.

Results

Field Assessment of Resistance

Between the planting day and the last measurement, agroclimatological conditions including air temperature, relative humidity, surface temperature and wind velocity did not differ considerably between seasons, but accumulated precipitation during the first season was 280 mm and 326 mm during the second season (Agromet 2023, Figure S1, Table S4).

When comparing the last late-blight scoring of each season, that means at 110 DAP, the first season (2017/18) and at 114 DAP in the second season (2018/19) (Fig. 1a and b), the genotypes exhibited varying levels of damage percentages between the different genotypes and seasons. The genotypes that showed lower percentage of damage compared to cv. Désirée (44.7%) in the first season were Azul (5.2%), Corahila Reina (7.0%), Azul Casposa (10.7%), Chilca-1 (18.0%), Murta (23.0%), SN-1 (25.2%) and Piku (28.0%). Otherwise, Papa Oro (55.5%) and Rosada Ojuda (82.2%) displayed higher scores of damage than the control cultivar Desirée. In the second season (Fig. 1b), five out of the seven genotypes mentioned at the first season with lower damage also showed low blight damage in the second season: Chilca-1 (2.0%), Piku (9.0%), SN-1 (10.0%), Azul Casposa (20.0%) and Azul (20.0%) compared to cv. Désirée (98.8%). Unexpectedly, Corahila Reina (67.5%) and Murta (80%) exhibited higher damage compared to the first season, but still lower than cv. Desirée. Additionally, Papa Oro (95%), Rosada Ojuda (100%) and the control cv. Désirée presented high damage percentages as in the previous season. Figure 1c illustrates the damage produced by the high-pressure infection that occurred during the second season especially in genotypes Papa Oro, Rosada Ojuda and cv. Désirée, all of which were strongly affected by late blight. Furthermore, genotypes Murta and Corahila Reina were more affected than the season before but showed better performance than the susceptible genotypes mentioned before.

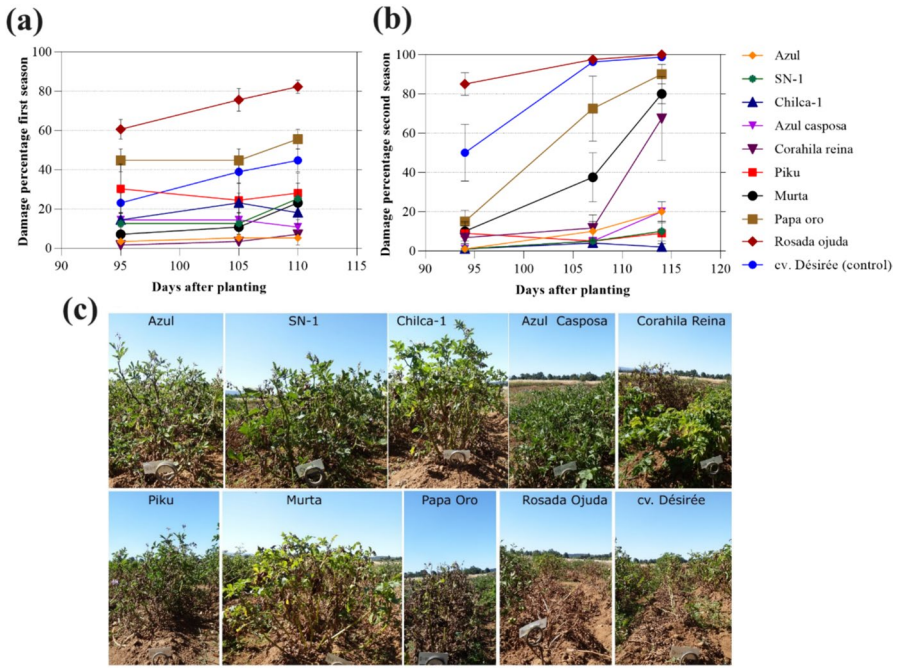

Fig. 1 Damage severity (%) of 10 potato genotypes in two seasons of field trials at the same location: **a** the first season 2017/2018 and **b** the second season 2018/2019. The graph shows means and standard error of the mean (SEM). **c** Pictures of the genotypes during the last scoring in the second season

Additionally, the slightly affected genotypes Azul, SN-1, Chilca-1, Azul Casposa and Piku still had green foliage at the last measurement.

In Table 1, the ANOVA for rAUDPC indicated a statistically significant difference among the genotypes, seasons and the G×E interaction (considering E as each season), where the mean square indicated that the major effect contributing to the resistance was the genotype factor. Additionally, there were no significant differences observed in the blocks nested within a season. In Fig. 2a and Table S2, the LSD of rAUDPC and the genotypes Azul (0.10), SN-1 (0.10),

Table 1 The ANOVA for rAUDPC considers data from both seasons together

Source	Sum of squares	Degrees of freedom	Mean square	F-distribution	*p* value
Genotype	4.2128	9	0.4681	39.46	0.0000
Season	0.1021	1	0.1021	21.65	0.0056
Genot*Season	0.7136	9	0.0793	6.68	0.0000
Block (season)	0.0236	5	0.0047	0.40	0.8479
Residual	0.5338	45	0.0119		
Total (corrected)	6.0005	69			

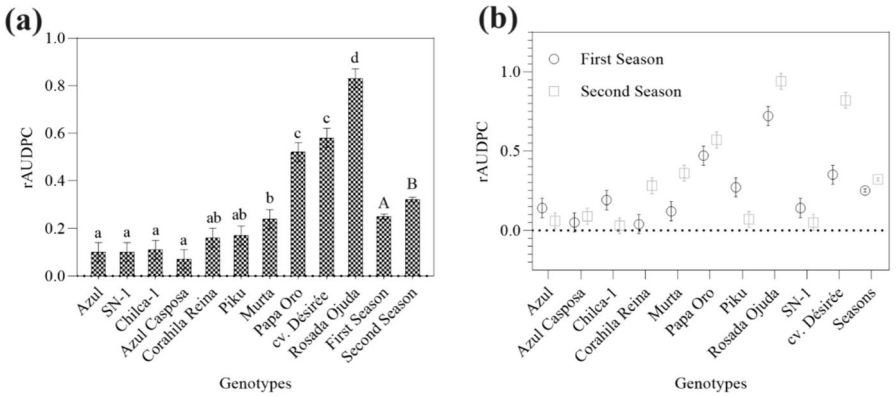

Fig. 2 Field trials. **a** The rAUDPC means with standard error bars (SE) for each genotype ($SE_{genotypes} = 0.04$) and season ($SE_{seasons} = 0.01$), considering both seasons ($n = 7$). LSD ($P < 0.05$). Different letters indicate statistically significant differences. **b** Performance of rAUDPC of potato genotypes in both seasons. The means and standard errors ($SE_{first} = 0.06$, $SE_{second} = 0.05$ and $SE_{seasons} = 0.01$) from the ANOVA consider $n = 7$ (first season ($n = 3$), second season ($n = 4$))

Chilca-1 (0.11), Azul Casposa (0.07), Corahila Reina (0.16), Piku (0.17) and Murta (0.24) were statistically significantly more resistant than cv. Désirée (0.58). On the other hand, Papa Oro (0.52) did not show statistically significant differences when compared to the control cv. Désirée, and Rosada Ojuda (0.83) did show statistically significant differences with more severe late-blight symptoms.

In Fig. 2b and Table S3, the performance of rAUDPC among the genotypes indicates that Azul, SN-1, Chilca-1 and Piku displayed lower values of rAUDPC for the second season compared to the first season, while Azul Casposa, Corahila Reina, Murta, Papa Oro, Rosada Ojuda and cv. Désirée exhibited higher rAUDPC values in the second season. All the scorings of genotypes indicate an increase in disease pressure in the second season compared to the first season. Additionally, it is noticeable that genotypes Azul, Azul Casposa and SN-1 stood out, showing more stability across the seasons.

Table 2 The ANOVA for arcsine of damage percentage for detached leaflet assay

Source	Sum of squares	Degrees of freedom	Mean square	F-distribution	*P* value
Genotype	2963.13	6	493.854	4.13	0.0088
Block	838.937	3	279.646	2.34	0.1077
Residual	2152.03	18	119.557		
Total (corrected)	5954.09	27			

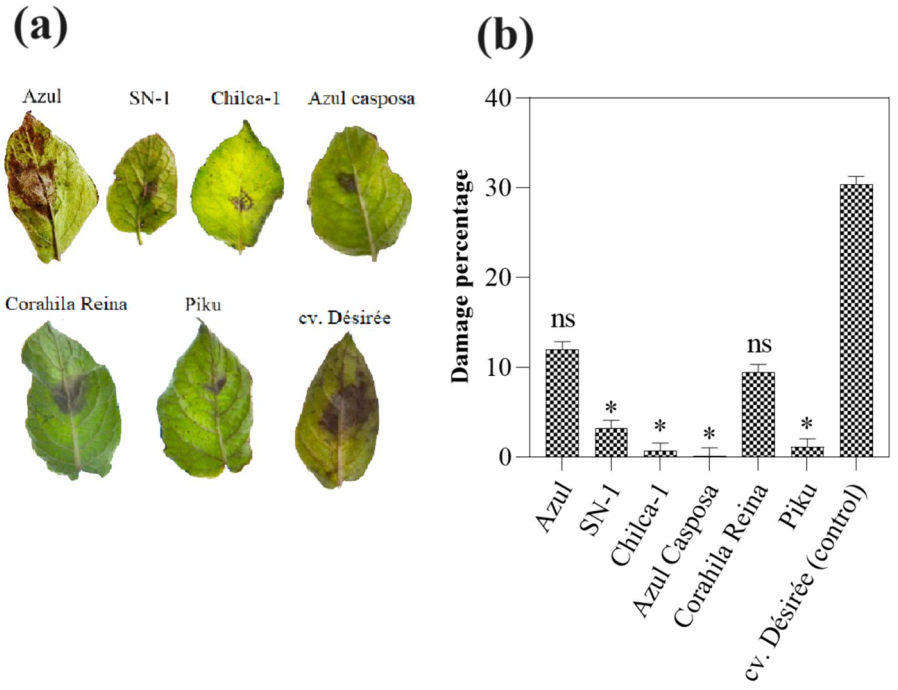

Fig. 3 Detached leaflet assay. **a** Leaflet inoculated with *P. infestans* at $5 \times 10.^5$ sporangia/mL after 7 days; **b** mean of damage severity (%) and standard error (SE = 0.91) on inoculated detached leaflets ($n = 4$) for each tested potato genotype. LSD ($P < 0.05$) using arcsine data transformation. The asterisk (*) indicates the statistically significant differences from 'cv. Désirée' with $P > 0.05$ (ns), $P \leq 0.05$ (*)

Lab Test Assessment of Resistance

The ANOVA for the detached leaflet assay (Table 2) revealed a statistically significant difference between genotypes and no significant differences observed in blocks. In Table S2 and Fig. 3b, the LSD analysis indicated that the genotypes Azul Casposa (0.11%), Chilca-1 (0.64%), Piku (1.11%) and SN-1 (3.16%) showed significantly lower damage percentage compared to cv. Désirée (30.35%), while Azul (11.92%) and Corahila Reina (9.43%) did not show statistically significant differences with the control. The images in Fig. 3a show the successfully *P. infestans*-inoculated leaflets.

Table 3 The ANOVA for arcsine of damage percentage for tuber assay

Source	Sum of squares	Degrees of freedom	Mean square	F-distribution	*P* value
Genotype	527.096	8	65.887	4.26	0.0066
Block	15.2695	2	7.63474	0.49	0.6193
Residual	247.359	16	15.4599		
Total (corrected)	789.724	26			

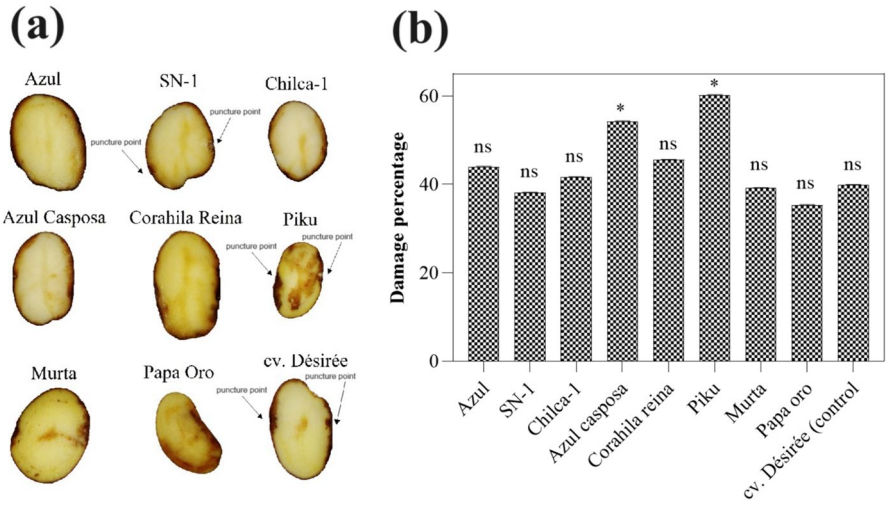

Fig. 4 Tuber assay. **a** Tuber symptoms of *P. infestans* after 30 days (inoculation at $5 \times 10.^5$ sporangia/mL). **b** Mean and standard error (SE = 0.16) of damage severity (%) on inoculated tubers (n = 3). LSD ($P < 0.05$) using arcsine data transformation comparing cv. Désirée with the genotypes. The asterisk (*) indicates that the genotypes were statistical significantly different from cv. Désirée ($P \leq 0.05$)

The ANOVA (Table 3) for the infection tuber assay also revealed statistically significant differences between the genotypes and no significant differences in blocks. In Table S2 and Fig. 4b, the LSD showed that genotypes did not differ statistically from the control cultivar in their scoring with exception of Piku (60.14%) and Azul Casposa (54.17%) who exhibited significantly higher tuber damage compared to cv. Désirée (39.79%). The images in Fig. 4a show the tubers successfully inoculated with *P. infestans*.

Correlation between the Tests

Pearson's test results indicate (Table S5) that the field trial with the detached leaflet assay demonstrated a significant correlation ($P = 0.0281$), characterised by a strong correlation ($r = 0.81$) and a high coefficient of determination ($r^2 = 65.19\%$). However, the combined field trials with the tuber test exhibited a weak negative correlation ($r = -0.46$), which was not statistically significant. Similarly, a negative, non-significant correlation ($r = -0.51$) was observed between the detached leaflet assay and the tuber test.

Discussion

Historically, late-blight infestations occur every year during the potato-growing seasons in the experimental site at the EEAA. Since that area has a temperate rainy climate characterised by high rainfall concentrated in the winter season

(González-Reyes and Muñoz 2013), sprinkler irrigation was applied during each growing season. The spores are carried by wind and rain to healthy plants, initiating the disease cycle again (Robinson et al. 2022). The geographical area is known for normal development of late blight disease. In both seasons, the randomised block design enables to observe the even distribution of late blight in the field assay (Fig. 1c).

The rAUDPC analysis reveals significant differences between seasons, with a notable increase in late-blight pressure during the second season, which was characterised by higher levels of rainfall compared to the first season (Figure S1; Table S4). The significant season effect observed in the present results can be attributed to natural infection without pathogen population management and aligns with Marhadour et al. (2013), who also associated higher disease pressure with more rainy seasons. The significant interaction G × E suggests considerable variation in rAUDPC under two different environmental conditions, variations that are consistent with the score of almost all evaluated genotypes. That observation is consistent with the results reported by Wulff et al. (2007) and Marhadour et al. (2013), who also identified significant interactions across multiple seasons at the same location.

The response to late-blight of six of the scored genotypes was as expected, as they displayed low rAUDPC values, which was in line with the low preselection scores. Genotype Murta presented the same response to late blight in the field then on the preselection score. However, Papa Oro and Rosada Ojuda exhibited high rAUDPC values, contrary to their initial screening results.

Even with the consistently low values among resistant native genotypes, the pressure from natural inoculum highlighted differences in rAUDPC values. Several investigations reveal resistances in potato, as Solano et al. (2014) documented 0.05 to 0.12 in four Chilean genotypes. In Peru, Wulff et al. (2007) found highly resistant genotypes with scores of 0.10 and 0.17. Muhinyuza et al. (2014) showed 20 genotypes ranging from 0.09 to 0.26 in Rwanda. In Spain, Meno et al. (2023) reported scores of about 0.01 to 0.05.

Considering the foliar damage scores of the control cultivar Désirée in this study, it presented comparable values to that reported by Haesaert et al. (2015) reaching up to 100% damage; conversely, Meno et al. (2023) reported a maximum of 10%. Regarding rAUDPC, cv. Désirée had higher values than those reported Solano et al. (2014) in Chile (0.16) and Marhadour et al. (2013) in France (0.27 to 0.43). The observed differences in cv. Désirée scores could be attributed to variations in the number of measurements, climatological conditions and/or *P. infestans* strains.

In the detached leaflet assay, Dorrance and Inglis (1997) reported scores in resistant potatoes ranging from 0.0 to 2.1% and susceptible cultivars from 35.3 to 55.1%, similar to those observed in cv. Désirée. Wang et al. (2020) observed a higher infected leaf area in cv. Désirée, ranging from 82 to 100%, using a different scoring method based on the presence of mycelium. The disparity in cv. Désirée scores observed in different investigations might also be related to the scoring method and distinct origins and strains of *P. infestans*. Halterman et al. (2010) examined *P. infestans* isolates collected from three countries, revealing complexity within the *ipiO* gene family and varying aggressiveness levels in the presence of *Rpi-blb1*.

Among the foliar-resistant genotypes characterised in the field, five of them (Azul, SN-1, Chilca-1, Corahila Reina, and Murta) could be classified as low to medium resistant in terms of tuber damage, as cv. Désirée did, according to the ECPGR 2023 classification. Stewart et al. (1992) used stolon absorption after 14 days and found lower damage percentages (1.7 to 15%) in cv. Désirée. The higher values in this study may be due to the longer incubation time and more invasive wounding method, as in the previous assay with a 15-day incubation, no symptoms were observed (data not shown). Świeżyński and Zimnoch-Guzowska (2001) also concluded that the expression of tuber resistance depends on testing conditions, so that it can be difficult to compare results as cultivar assessment data from various countries could differ considerably. The genotype Rosada Ojuda was excluded from the tuber resistance test because brown and purple flesh areas overlapped, rendering differentiation inaccurate. However, an alternative to test pink or purple flesh could be tested using a sliced tuber test measuring mycelium growth and sporulation, as described by Bachmann-Pfabe et al. (2019).

Considering the correlation analysis between the field trial and the detached leaflet assay highlights a strong relationship, confirming the foliar resistance of genotypes. Michalska et al. (2011) also reported a significant and strong relationship between infected detached leaflet assays and rAUDPC ($r^2 = 77.4\%$) in the field. Similarly, Shrestha et al. (2019) found a significant and strong correlation ($r = 0.70$) between detached leaf assays and field resistance assays. Douches et al. (2002) found no correlation between the resistance of the tubers and the resistance of the foliage for 28 evaluated potato-breeding lines, which is consistent with the results obtained in this research. Genes such as *Rpi-abpt* and *R3a* confer foliage-specific resistance (Park et al. 2005) and QTLs have been detected for organ-specific resistance (Juyo Rojas et al. 2019), which could explain the lack of correlation. Interestingly, a recent review suggests that tuber blight resistance occurs independently of foliage blight resistance, while other studies suggest a correlation. Therefore, it is unclear if foliage and tuber resistance are genetically linked (Blossei et al. 2022). The presence of partial resistance found in the different genotypes may be attributed to the interplay of multiple *R* genes responding to a complex virulence pattern associated with the 11 *Avr* genes identified by Sandoval et al. (2019) in most isolates from southern Chile. Therefore, the involved genes should be specific resistance genes against late blight that could contribute as candidates for further investigations in late blight resistance and the development of resistant potato varieties.

Conclusions

The diversity in *Solanum tuberosum* ssp. *tuberosum* Chilotanum group at the UACh Potato Genebank is a source of resistance genes against late-blight disease. The field assay showed seven genotypes (Azul, SN-1, Chilca-1, Azul Casposa, Corahila Reina, Piku and Murta) that indicated more foliage resistance to late blight in the field than cv. Desirée. Among these genotypes, four (Azul Casposa, Chilca-1, Piku and SN-1) demonstrated better performance in resistance on the detached leaflet assay as well. Furthermore, five of the foliar-resistant genotypes (Azul, SN-1,

Chilca-1, Corahila Reina, and Murta) could be considered to have low to medium resistance compared to cv. Désirée in terms of tuber resistance. Based on the shown data, SN-1 and Chilca-1 were candidates to continue working with late blight resistance in breeding programs, as they present good foliar and low to medium tuber resistance. For gene resistance characterisation and as a source of foliar resistance genes against late blight, the genotypes Azul Casposa, Chilca-1, Piku, and SN-1 were suggested as candidates for further investigations.

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Declarations

Conflict of Interest The authors declare no competing interests.

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