Heritability of resistance to potato late blight in an F1 population of elite potato cultivars[1]

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ABSTRACT

Phytophthora infestans is the most important disease in potato crops. Its control is based on the use of chemical products that have developed pathogen resistance and high economic and environmental impacts. To reduce these effects, the use of plant varieties or cultivars resistant to this pathogen has been proposed. The aim of this study was to evaluate the heritability of resistance to this pathogen in a population of elite *Solanum phureja* genotypes. In this study, 1,355 clones with three replicates from 20 families were included in the evaluation. Heritability was assessed in the broad and narrow senses. Results of the relative area under the disease progress curve varied between 0.08 and 0.64, indicating that the population contains genes that code for resistance. Heritability in both directions (narrow 0.022 and broad 0.255) showed significant differences, indicating an influence of dominance genetic effects and environmental effects. Thus, to use these genotypes in potato breeding programs, hybridization methods should be used instead of selection methods.

Keywords: severity; area under the disease progress curve; genetic progress; incidence.

INTRODUCTION

Potato is considered one of the most important crops worldwide, with an annual production of close to 402 million tons (FAOSTAT, 2016). Its importance in Colombia lies in the fact that it represents food security, besides being an important link in the economy, due to the use of workforce in cultivation and production, generating about 20 million wages per year (Cotes & Ñústez, 2014; Lara & Chaparro, 2017).

The production of this crop has mainly been threatened by *Phytophthora infestans* (Mont.) de Bary, the causal agent of late blight, one of the most critical diseases in potato cultivation. This is even more critical if we consider that the most susceptible cultivars of *Solanum tuberosum* L. and *Solanum phureja* Juz et Buk to the microorganism are the ones that are most widely cultivated worldwide, generating a gap between potential and real yields (Forbes & Pérez, 2008; Fry & Grünwald, 2010; Forbes, 2012; Forbes *et al.*, 2014).

If the infection occurs in the early stages of crop development, losses in production can reach up to 80% (Tsedaley, 2014; Berhan, 2021). The control of this disease involves from 10 to 16 applications during the crop cycle, representing between 10 and 20% of the production cost (Haverkort *et al.*, 2009). In addition to these costs, the environmental costs generated by using agrochemicals must be considered (Fry & Grünwald, 2010; Kromann *et al.*, 2009; Restrepo & Ñústez, 2014). Therefore, the use of resistant materials is proposed to correct the consequences that the application of chemical products generates (Kromann *et al.*, 2011; Lagos *et al.*, 2021).

In this sense, the knowledge of the genes action that controls characteristics of interest is essential in breeding programs. This knowledge, however, must be based on the evaluation of heritability in the population of interest, determining the similarities between the progenies and their parentals. This is a population characteristic that expresses the ability of a material to transmit a character and how it varies due to environmental or genetic factors (Cruz & Regazzi, 2001; Poehlman & Allen, 2003; Ruales *et al.*, 2007; Guillen *et al.*, 2009; Tinjacá, 2010).

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Accordingly, the aim of this research was to evaluate the heritability of the resistance to *P. infestans* in an F1 population obtained from elite genotypes of the diploid potato-breeding program of Universidad Nacional de Colombia.

MATERIALS AND METHODS

Location

The evaluation of the heritability of resistance to *P. infestans* was carried out in plots located in the Agricultural Research Station Paysandú of Universidad Nacional de Colombia – Sede Medellín, located in Santa Helena, department of Antioquia, at an altitude of 2,671 meters. During the development of the research work, standard agronomical management such as fertilization and weed control was carried out.

Plant material

A total of 1,355 individuals from 20 full-sib families of potato (Table 1) were obtained in a mesh house through controlled pollination using the methodology proposed by Grisales *et al.* (2008). The sexual seed was established under field conditions of the Agricultural Research Station Paysandú to produce mini-tubers. The tubers used for sowing corresponded to the ones obtained from sexual seed. The following eight elite potato cultivars with different resistance levels to *P. infestans* were used as parents. Cultivars Criolla Ocarina (Rodríguez & Tinjacá, 2015) and Criolla Galeras (Rodríguez *et al.*, 2014), show moderate resistance, genotypes B09-3-8 and 10-126-8 have high potato blight resistance, cultivars Paola and Primavera show very high resistance to late blight, and cultivars Violeta and Paysandú have an intermediate resistance level to late blight (Cotes & Ñústez, 2014). The potato breeding program of Universidad Nacional de Colombia provided these materials.

P. infestans severity

The severity was established visually using a scale proposed by Henfling (1987). The severity level in the scale was assigned to evaluate the presence of typical symptoms of *P. infestans*, such as brown spots with wet appearance and the presence of sporulation in the leaves (Fry & Grünwald, 2010). In addition, an inspection of the plant foliage was carried out thoroughly because some of the symptoms were not observed in plain sight, underestimating the affected area (Forbes *et al.*, 2014; CIP, 2014). Weekly evaluations were made (Forbes *et al.*, 2014; Forbes & Pérez, 2008), beginning 62 days after sowing (DAS) and extending until completing 103 DAS, obtaining seven evaluation times.

Experimental design and statistical analysis

The experimental design was established as a completely randomized block design with three blocks. Each block includes 1,355 plots composed of five plants each, established with a distance of 0.3 m between plants and 0.9 m between hills. The inoculum pressure was guaranteed by the establishment of random plots in each hill of *S. phureja* cv. Criolla Colombia (susceptible control variety).

Susceptibility assessment

Plant susceptibility was evaluated using the relative area under the disease progress curve (AUDPCr). It was expressed as the ratio between the value of the observed area under the disease progress curve (AUDPC) and the average AUDPC of the neighbor susceptible control variety at the radiuses of 5, 10, 15, or 20 m obtained through the kriging method using the inverse distance weighted interpolation. This estimation was performed in the R statistical program of the R Core Team of 2016, using the gstat package (Pebesma, 2004; Gräler *et al.*, 2016).

Table 1: Full-sib families established in the study. The first name used in the crosses corresponds to the female parent and the second to the male parent

ID	Families	Ind	ID	Families	Ind
1	Galeras × Paola	82	11	Paysandú × Violeta	44
2	Ocarina × Paola	76	12	10-126-8 × Primavera	60
3	Violeta × Paola (*)	150	13	Paola × Primavera (*)	72
4	Paola × Violeta (*)	51	14	Ocarina × Violeta (*)	62
5	Primavera × Ocarina (*)	128	15	Paysandú × Paola	95
6	10-126-8 × Violeta	69	16	10-126-8 × Paola	66
7	Primavera × Violeta	60	17	Galeras × Primavera	97
8	Violeta × Ocarina (*)	63	18	B09-3-8 × Paola	28
9	Galeras × Violeta	55	19	Ocarina × Primavera (*)	19
10	Primavera × Paola (*)	74	20	Galeras × Ocarina	4

(*) Families with direct and reciprocal crossing

Ind: Number of individuals

Natural logarithm ($\log_e$) transformation of the data was made to perform de genetic analysis, and the statistical model used is the following:

$$\log_e(\mathbf{Y} + 0{,}01) = \mathbf{1}\mu + \mathbf{X}\boldsymbol{\beta} + \mathbf{Z1}\boldsymbol{\alpha} + \mathbf{Z}2\delta + e$$

where **Y** is a vector of size nx1 of observations, with *n* being the number of observations of AUDPCr, **1** is a vector of size nx1 with every element equal to unity, μ is an overall mean, **â** is a vector of size px1 of fixed effects, with *p* being the number of levels of the fixed effects of the block, **á** is a vector of size qx1 of random additive genetic effects of the individual, with *q* being the number of individuals in the pedigree, and **ä** is a vector of size dx1 of dominant genetic random effects of the individual, with *d* being the number of individuals in the pedigree. **X**, $\mathbf{Z}_1$, and $\mathbf{Z}_2$ are incidence matrices that relate the observations with the fixed, genetic breeding value and genetic dominant effects, respectively, and **e** is a vector of size nx1 of residual random effects. The random effects have variance σ^2_A, σ^2_D and σ^2_E for breeding value, genetic dominant, and residual effects, respectively.

Resistance heritability to P. infestans

The AUDPCr variable was used to calculate heritability in the broad sense (H^2), heritability in the narrow sense (h^2), and the ratio between the additive and the dominant variances. Additionally, the expected response for individual selection and half-sib and full-sib families was estimated. For individual selection, the equation $R = ih^2\sigma^2_p$ was used. For the sib family selection, the following equation was used (Falconer & Macray, 1996):

$$R = ih^2 s_p^2 \frac{1 + (n - 1)r}{\sqrt{n[1 + (n - 1)t]}}$$

where *r* is 0.25 for half-sib families and 0.5 for full-sib families, *n* is equal to 100 individuals, *t* is the intraclass correlation obtained as $t = \frac{\frac{1}{4}\sigma^2_A}{\sigma^2_A + \sigma^2_D + \sigma^2_E}$ and $t = \frac{\frac{1}{2}\sigma^2_A + \frac{1}{4}\sigma^2_D}{\sigma^2_A + \sigma^2_D + \sigma^2_E}$ for half-sib and full-sib families selection methods, respectively, and *i* is the selection intensity (selection differential in standard measure).

The analysis was performed in the R statistical program of the R Core Team of 2016, using the MCMCglmm package (Hadfield, 2016). The Bayes estimates used correspond to the median and the mean of the posterior distribution of the parameter, and subsequently, its respective highest posterior density (HPD) interval of 95% probability was obtained. For this purpose, the CODA package was used (Plummer *et al.*, 2015). Finally, a matrix associated with the genetic effects was constructed using the nadiv package (Borregaard *et al.*, 2014).

RESULTS AND DISCUSSION

Description of the study population

The lowest value of the diseased leaf area (DLA) at the last evaluation was 8% recorded in family 10, while the highest values were observed in the control, with an average value of 71%, followed by family 19 with an average value of 38% of the leaf area affected by the disease (Table 2).

These results show the susceptible performance of the control and indicate that the study population contains resistance genes that maintained a low severity response of the disease, even at the end of the crop cycle.

The family that showed the highest proportion of progeny with severity equal to zero corresponds to family 16 (7% of the population without infection). On the other hand, family 13 showed the highest proportion of genotypes with an affected leaf area between 0% and 5% (85% of the population in this scale range).

In the ranges 5% to 30% and higher than 30% of the average leaf area affected by the disease, family 20 presented the highest average percentage of individuals (75% and 25%, respectively), followed by the control with 71% of the individuals with a DLA between 5 and 30% and 24% with DLA higher than 30%. Conversely, in families 4, 10, 12, 13, 14, and 19, no individuals are reported in the category between 30 and 100% of the leaf area affected by the disease.

The experimental results allow concluding that a good disease level was reached on the field experiment due to severity level variations between zero (0) and 100% of the affected leaf area found in the population. It was also possible to observe in the susceptible control cultivar high levels in the severity scale. On the other hand, 96% of the clones were affected in 30% or less of the leaf area.

It is noteworthy that the results of this research with values of zero disease incidence should show that families contain individuals with genes that code for vertical resistance to the pathogen like that expressed by Grisales & Cotes (2018). Thus, in this population, the characteristic of resistance to the pathogen is inherited by the progeny, allowing the use of the parents in potato plant breeding programs by hybridization as expressed by Zúñiga *et al.* (2000) and Orozco (2012).

AUDPCr

The mean AUDPC value concerning the susceptible check cultivar is between 0.08 and 0.64 (Table 2), so the clones evaluated show higher resistance to the disease compared to the control, except for family 20.

Bisognin (2002) suggests a susceptibility classification of the clones as follows: clones with AUDPCr values between 0.0 and 0.20 can be considered highly resistant,

Table 2: Mean values, standard deviation (SD), and coefficient of variation (CV) for late blight severity at the last evaluation, percentage of affected individuals for the disease according to the severity scale used, and relative area under the disease progress curve (AUDPCr) in relation to the susceptible check cultivar in the families evaluated

ID	Families		Severity			Percentage of progeny				AUDPCr		
			Mean	SD	CV	0	> 0 - 5	> 5 - 30	> 30 - 100	Mean	SD	CV
1	Galeras	Paola	17.24	13.85	80.33	1.23	45.87	51.97	0.93	0.20	0.19	92.85
2	Ocarina	Paola	18.88	14.98	79.35	3.03	49.66	44.28	3.03	0.31	0.41	131.76
3	Violeta	Paola	12.31	11.99	97.44	2.76	65.83	30.84	0.56	0.13	0.19	148.54
4	Paola	Violeta	13.96	12.20	87.38	0.00	68.43	31.57	0.00	0.10	0.08	78.29
5	Primavera	Ocarina	20.33	16.52	81.28	1.48	38.05	55.76	4.71	0.33	0.37	110.89
6	10-126-8	Violeta	16.26	13.77	84.71	3.50	57.93	37.34	1.22	0.18	0.25	142.02
7	Primavera	Violeta	17.65	16.11	91.28	0.00	61.49	37.92	0.60	0.18	0.17	98.58
8	Violeta	Ocarina	17.89	10.76	60.16	0.00	50.80	48.19	1.01	0.19	0.20	100.41
9	Galeras	Violeta	22.40	14.82	66.18	0.00	27.10	69.87	3.03	0.28	0.26	91.98
10	Primavera	Paola	7.56	7.40	97.95	2.96	79.04	18.01	0.00	0.10	0.13	133.31
11	Paysandú	Violeta	12.14	13.03	107.34	3.70	65.94	29.48	0.88	0.10	0.20	186.15
12	10-126-8	Primavera	8.17	5.60	68.64	0.63	82.73	16.64	0.00	0.09	0.07	81.01
13	Paola	Primavera	7.76	6.80	87.65	3.06	84.56	12.38	0.00	0.08	0.09	102.27
14	Ocarina	Violeta	16.01	9.13	57.06	2.94	52.28	44.78	0.00	0.15	0.12	78.21
15	Paysandú	Paola	12.53	13.06	104.23	1.35	67.93	30.36	0.36	0.14	0.18	131.06
16	10-126-8	Paola	12.80	14.50	113.24	6.75	61.94	28.19	3.12	0.19	0.29	151.73
17	Galeras	Primavera	14.21	10.90	76.73	3.41	46.64	49.52	0.42	0.14	0.16	120.92
18	B09-3-8	Paola	16.58	18.40	111.00	3.70	48.91	44.71	2.67	0.15	0.20	134.69
19	Ocarina	Primavera	12.17	6.74	55.40	0.00	50.00	50.00	0.00	0.14	0.12	85.67
20	Galeras	Ocarina	37.50	23.63	63.01	0.00	0.00	75.00	25.00	0.64	0.52	80.31
Overall population			14.56	13.30	91.37	-	-	-	-	0.17	0.23	136.00
Check susceptible variety			71.00	17.49	24.63	0.00	5.88	70.59	23.53	-	-	-

genotypes with AUDPCr between 0.21 and 0.56 are moderately resistant, and the ones considered susceptible correspond to those with AUDPCr values higher than 0.56. Hence, 80% of families evaluated in this study should be classified as highly resistant to the disease, and only families 2, 5, 9, and 20, as moderate resistant. The population studied in this research has genes of resistance to late blight, but considering that some of the descendants reached high AUDPCr values, it could be expected that the population also possesses a few recessive genes for resistance.

Heritability of the resistance to P. infestans

The results of this study indicate that the heritability parameter of the population of interest in each of their expressions showed statistically significant differences (Table 3).

The heritability values should be classified as low if values are lower than 0.25, medium or moderate when these are between 0.25 and 0.50, or high if values are higher than 0.50 (Ruales *et al.*, 2007). Thus, the heritability in the population assessed in the narrow sense or additive heritability (h^2_a), with a mean value of 0.0227, is considered low. On the other hand, the heritability in the broad sense or genetic heritability (H^2), with a value of 0.25511, is considered medium or moderate.

Regarding the heritability of resistance characteristic to *P. infestans* in tetraploid potatoes under field conditions, an H^2 value of 0.79 was reported; meanwhile, for h^2, a value of 0.78 was registered (Haynes *et al.*, 2007).

Table 3: Narrow- and broad-sense heritability, estimated variance components, and 95% highest posterior density (HPD) intervals for the AUDPCr variable in the study population

Estimated parameters	Bayes estimates		HPD 95%	
	Mean	Median	Lower	Upper
Additive variance (σ^2_a)	0.00587	0.0014	< 0.0001	0.09145
Genetic variance ($\sigma^2_a + \sigma^2_d$)	0.05911	0.05933	0.03974	0.07713
Variance of the error (σ^2_e)	0.18928	0.18917	0.17636	0.20222
Additive heritability (h^2_a)	0.02274	0.00553	< 0.0001	0.09145
Genetic heritability (H^2)	0.25511	0.25465	0.20144	0.30915
Additive/Dominant relation	0.11811	0.02259	< 0.0001	0.51336

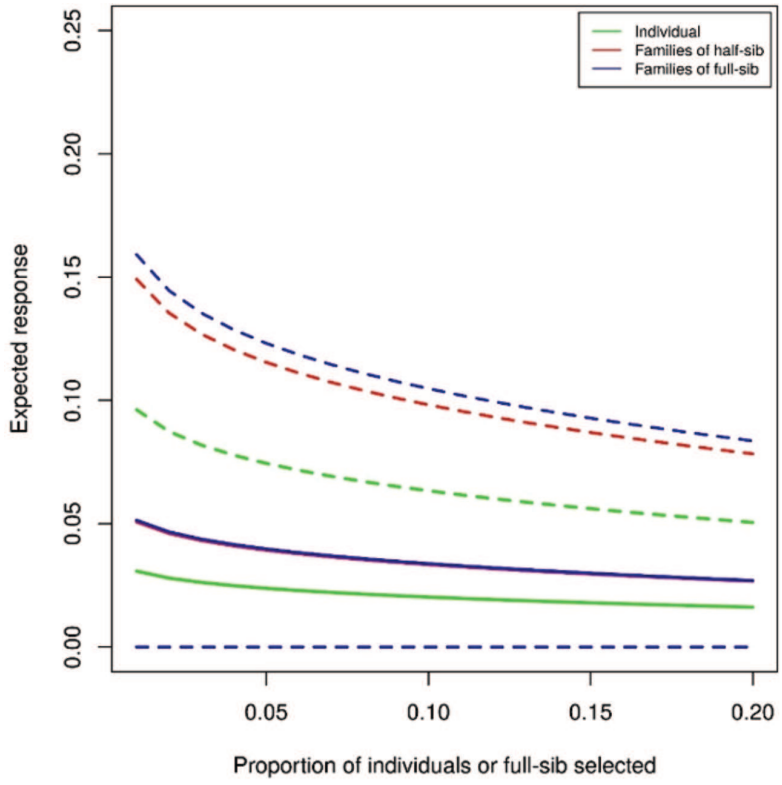

Figure 1: Expected response for the area under the disease progress curve relative to the susceptible check cultivar under different selection methods for the study population. Results are presented as the relative area under the disease progress curve (AUDPCr). Solid lines show the Bayes estimate and dashed lines display the highest posterior density at 95%.

On the other hand, in diploid potatoes, narrow-sense values of 0.78 and broad-sense values of 0.79 have been found (Haynes & Christ, 2006), Costanzo *et al.* (2004) report in the broad sense, a heritability value in diploid potatoes of 0.67.

These studies show a significant genetic component, allowing to establish potato breeding material based on selection methods. This is because, in this population, it is possible to transfer the characteristic of interest to the new generations that can guarantee selection success (Haynes & Christ, 1999; Orozco *et al.*, 2013). However, in the population used in this research, it is not possible to obtain gain in the genetic improvement processes by selection methods. Furthermore, the additive genetic variance was likely exhausted, but it is also possible to include these parents in genetic improvement processes through hybridization methods.

According to Poehlman & Allen (2003), a characteristic such as resistance to diseases is highly influenced by the environment, presenting low heritability. Ñústez (2011) expresses that the heritability results are due to the genetic variation in the population and the environment where the crop grows. Just as the results of this study, in terms of heritability in the broad sense for resistance to *P. infestans* in diploid potatoes, Tinjacá (2010) reports values of 0.40, and in the narrow sense, values of 0.13, indicating that in the study population, there is a strong influence of non-additive effects on the characteristic assessed.

Considering that the heritability values in the broad sense obtained have the highest value (0.255) compared with the heritability in the narrow sense (0.022), it is possible to conclude, in agreement with Moncayo *et al.* (2019), that in the study population, phenotypical variations are due to dominance genetic effects and not to additive effects. This was confirmed by the results obtained for the relationship between the additive variance and the dominant variance with a value of 0.11.

Great efforts should be made in selection pressure to achieve a low genetic advance (Figure 1), which may be due to the lack of action of non-additive genes, as well as to environmental effects (Soomro, 2010; Orozco *et al.*, 2013), confirming that the plant breeding method recommended for the population under study, should use parents in hybridization program rather than the selection of individuals.

CONCLUSIONS

The disease was developed in the study area due to finding in the population, severity level variations between zero (0) and 100% of the affected leaf area. It was also possible to observe in the susceptible control high levels in the severity scale.

About 96% of the clones were affected in 30% or less of the leaf area, indicating high resistance in the evaluated clones.

With a value of 0.022, the heritability in the narrow sense is considered low, while the heritability in the broad sense with a value of 0.255 is deemed average, indicating that phenotype variations are due to dominant effects in the study population.

In the study population, the process of plant breeding for resistance to P. infestans should focus on hybridization rather than selection of materials.

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