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Inheritance of early blight resistance in diploid potatoes

Rodomiro Ortiz[1], Carlos Martin, Masaru Iwanaga[2] & Hebert Torres
International Potato Center (CIP), Lima, Peru; [1] Author for correspondence. Current address: International Institute of Tropical Agriculture (IITA), c/o Lambourn, Carolyn House, 26 Dingwall Road, Croydon, CR9 3EE, England; [2] Current address: International Plant Genetic Resources Institute (IPGRI), Via delle Sette Chiese 142, 00145 Rome, Italy

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Abstract

Early blight (*Alternatia solani*) is a fungal disease in hot and humid environments, which causes leaf, stem and tuber lesions. Early blight resistance should be incorporated into potato cultivars because the fungicide spraying is an expensive solution for developing countries. The diploid cultivated species *Solanum tuberosum* group *Phureja* and group *Stenotomum* are sources of resistance alleles. The elucidation of the inheritance for early blight resistance must help to decide what could be the best breeding procedure to improve this diploid germplasm and transfer the resistance to the tetraploid level. Three experiments were carried out under controlled and field conditions to determine the heritability of this trait using nested and diallel mating designs with haploid, species and haploid-species hybrids. The narrow-sense heritability estimates were relatively high (0.64 – 0.78). This means that additivity was the most important type of gene action for determining resistance to early blight at the diploid level. The results suggested that diploid parents showing highest levels of resistance, throughout the cycle of disease development, can be used in 4x × 2x crosses to obtain resistant tetraploid progenies to this fungal disease.

Introduction

Early blight is an important disease in many tropical and subtropical countries with high temperatures (20–25° C) and moderate to high humidity. The causal organism is the fungus *Alternaria solani* Sorauer, which on potato causes leaf, stem and tuber lesions. It usually attacks lower and older leaves in mature plants, but in tropical countries it can attack at earlier stages. The lesions often coalescence and lead to blighting and after six weeks complete defoliation may occur.

It is important to incorporate early blight resistance into potato cultivars because the fungicide spraying is an expensive solution for developing countries. Resistance alleles have been identified in the diploid cultivated potatoes of the Andes *Solanum tuberosum* Group *Phureja* and Group *Stenotomum*.

Herriot et al. (1986) determined the narrow sense heritability as 0.82 for early blight resistance using offspring-mid parent regression on an individual plant basis in a diploid *Solanum tuberosum* group *Phureja* – group *Stenotomum* population. Similarly, Mendoza et al. (1986), working a the tetraploid level, obtained an average narrow sense heritability of 0.70. These high estimates suggested that rapid progress in resistance could be made with selection. Al-

so, Mendoza et al. (1986) found a positive phenotypic correlation between the degree of resistance and vine maturity, i.e. clones with large length of the growing period had the highest levels of early blight resistance. The aim of the present work was to determine the inheritance of early blight resistance in a diploid population derived from crosses among haploids (extracted from tetraploid cultivated potatoes group *Tuberosum* and group *Andigena*) and cultivated and wild diploid tuber-bearing *Solanum* species. The source of resistance in this population was from the diploid species *Solanum tuberosum* group *Phureja* – group *Stenotomum*.

Materials and methods

Three experiments were carried out to estimate the type of inheritance of early blight resistance.

During 1986 different types of crosses (resistant × resistant, resistant × susceptible, susceptible × resistant and susceptible × susceptible) were tested under controlled conditions in La Molina (coast) and San Ramon (mid-elevation tropics). The crosses used in both experiments were made following a nested mating design (North Carolina Design I) using 10 male parents and each of them crossed with 4 female parents. Four of the male parents were selected as early blight resistant clones at North Carolina (USA) by Dr. F.L. Haynes while the other diploid parents from other breeding populations were susceptible to early blight.

In 1987, 30 families were obtained using six parents (one early blight resistant clone selected by Dr. F.L. Haynes in North Carolina) which were crossed following a diallel mating design (Table 1). The reciprocal crosses were included but not the selfed progenies.

The first experiment under controlled conditions was carried out in a greenhouse at La Molina. True potato seed (TPS) from the 40 families (100 seeds of each one) was sown in trays; after 30–40 days the seedlings were inoculated by spraying them with an inoculum suspension of 1500–2000 spores/ml and kept inside large plastic bags for 4 days at 22–25° C.

The second experiment used the same 40 progenies of the first experiment and these were sown in beds of 10 m^2 at San Ramon. After 30–40 days the plants were inoculated and beds were covered for 4 days with a plastic sheet.

The third experiment was carried out at field conditions in San Ramon. Thirty progenies were sown, but one of them did not germinate, so only 29 could be used for the analysis. Plants were obtained from TPS in the screenhouse. A randomized complete block design with three replications was used for the evaluation of field resistance to early blight. Field plots were single rows of 75 cm by 9 m with plants spaced 40 cm apart. A 2×10^3 spores per ml suspension of *A. solani* was sprayed on the seedlings' leaves after 30 days of planting. Two weeks later they were reinoculated for a good infection. Open pollinated seed of a susceptible cultivar (DTO-33) was used in the experiments as a control for disease development.

In the two experiments under controlled conditions the data for early blight resistance were taken 4 and 6 days after inoculation (Martin et al., 1986).

Table 1. Diploid parents of the diallel cross experiment.

Clone	Breeding population[1]	Species[2]	EBR[3]
FH-92	NCSU-Heat adaptation	phu-stn	susceptible
FH-122	NCSU-Early blight	phu-stn	resistant
MI-17.12	CIP-Bacterial wilt	adg, tbr, spl, phu, chc	[4]
MI-49.10	CIP-Bacterial wilt	adg, tbr, spl, phu	susceptible
381328.18	CIP-Root knot nematode	phu-stn, spl	susceptible
381348.7	CIP-Root knot nematode	phu-stn, spl, tbr	susceptible

[1] NCSU = North Carolina State University; CIP = Centro Internacional de la Papa.

[2] Species abbreviations according to Huaman & Ross (1985).

[3] Early blight resistance.

[4] This clone was not evaluated for early blight resistance due to infection with virus and subsequently loss from the breeding population.

In the field's experiment data in each replication were collected 15, 30 and 45 days after inoculation. In the three experiments a 1 (lowest score of early blight infection) to 9 (highest score) scale was used. This scale was based on the relative number of lesions and percentage of defoliation.

The statistical analyses for the experiments under controlled conditions were done following the analysis of variance for the Design I (Hallauer & Miranda, 1981). The field experiment was analyzed using the diallel cross analysis of variance (Martinez Garza, 1975). Regression analyses were carried out using the data of the diallel experiment. The early blight score and days after inoculation were the dependent (Y) and independent (X) variables of the regression model. Therefore, a clone with a low regression coefficient (b) was considered as a promising progenitor to develop early blight resistant offspring.

Results and discussion

The results of the experiments under controlled conditions grouped by type of mating are reported in Table 2. Progenies had resistance to early blight when the female parents were resistant to this disease. Conversely, progenies from susceptible female parents had lower levels of resistance or were susceptible (e.g. results from San Ramon). This might indicate a maternal type of inheritance for early blight resistance. A similar response was found with another *Alternaria* species, *A. alternata*. This fungus produces a tentoxin that binds to one subunit of chloroplast-coupling factor encoded by the chloroplast DNA (Steel et al., 1976). The sensitive plants to tentoxin do not develop a normal photosynthetic apparatus and produce white leaves in the presence of the toxin.

Based on these results, the field experiment using a diallel cross with reciprocals was carried out to elucidate whether early blight resistance was maternally inherited or not. The analysis of variance is shown in Table 3. The crosses and maternal effects were not statistically different at 15 and 30 days after inoculation. However, they were significantly different at 45 days after inoculation. Even in this date the maternal effects were not significant. At 45 days only general combining ability (GCA) effects were highly significant. This result clearly demonstrated that early blight resistance at diploid level was not maternally inherited. Furthermore, this was supported by the production of early blight resistance haploid-species hybrids, in which the female parent was susceptible to this disease (data not shown).

The analysis of variance for the experiments un-

Table 2. Early blight resistance in different types of matings evaluated after 6 days of inoculation under controlled conditions (La Molina & San Ramon, 1986).

Type of mating	Early blight resistance			
	San Ramon		La Molina	
	% Resistance[1]	Mean[2]	% Resistance	Mean
Resistant × Resistant	25	5.1	100	3.7
Resistant × Susceptible	35	4.2	60	4.1
Susceptible × Resistant	0	5.5	17	4.6
Susceptible × Susceptible	0	5.2	25	4.4

[1] % of progenies with less than 3 in 1–9 early blight resistance scale.
[2] of progenies using a 1 (resistant) to 9 (susceptible) scale.

Table 3. Analysis of variance and heritability for early blight field resistance using a 6 × 6 diallel (San Ramon, 1987).

Source of variation	d.f.	Mean Square	
		30 days after inoculation	45 days after inoculation
Replications	2	1.94 ***	0.72 *
Crosses	28	0.13	0.46 **
GCA	5	0.33	1.57 *
SCA	9	0.07	0.14
Maternal effects	5	0.14	0.26
Reciprocals	9	0.32	0.30
Error	56	0.20	0.21
Coefficient of variation (%)		16.53	14.34
Mean		2.74	3.19
Narrow sense heritability		0.14	0.64

*, ** and *** indicate significance at the 0.05, 0.1 and 0.001 levels.

der controlled conditions at La Molina and San Ramon (Table 4) indicated that only the differences between males were significant in both evaluation dates. This confirmed the previous results that demonstrated that additivity was the most important type of gene action for determining resistance to early blight in diploid potatoes.

Narrow sense heritability estimates were high in both controlled and field experiments. This suggests that rapid progress can be made by mass selection or phenotypic recurrent selection. This was corroborated by the results of Table 2, i.e., a high percentage of resistant progenies should be obtained by crossing two parents with resistance to early blight. Furthermore, early blight resistance can be transferred from the diploid to the tetraploid level through the use of 2n gametes (Herriot et al., 1990).

The hybrid progenies evaluated in the field at San Ramon showed late maturity. Therefore, it is important to incorporate earliness to this material but keeping high levels of resistance to early blight. This can be done by using haploids from early blight resistant tetraploids.

The breeding values of each clone used in the diallel cross are indicated in Table 5. The best parental material was MI-17.12, which showed negative and significant GCA estimates for early blight resistance. This haploid-species hybrid developed at the International Potato Center (CIP) was better than the previously resistant clone FH-122, which was selected by Dr. F.L. Haynes from the diploid *Phureja-Stenotomum* population in North Carolina. FH-122 had a negative but non significant GCA estimate for early blight resistance. The hybrids 381348.7 and MI-49.10 were the parental materials with progenies having the lowest levels of resistance to early blight.

Fig. 1 illustrates the development of the disease for each parent, which was determined by pooling the performance of their progenies. It was clear that at early stages of disease development (15 days after inoculation) the susceptible parent 381348.7 had the highest level of resistance. However, this clone and MI-49.10 had the highest regression coefficient when their early blight score was regressed on days after inoculation.

It may be possible to select promising progenitors to develop early blight resistant clones by evaluating their progenies at different stages of disease development. We suggest to select the resistant parents based on their breeding values (i.e. lowest early blight resistance score) in the last evaluation date combined with the lowest regression coefficient for the development of the disease. In this regard, MI-17.12 combined both attributes.

The results also suggested that different mechanisms are functioning at different stages of plant development to determine early blight resistance. For

Table 4. Combined analysis of variance for a nested disign (North Carolina's Disign I) and heritability for early blight resistance evaluated under controlled conditions 4 and 6 days after inoculation (La Molina & San Ramon, 1986).

Source of variation	d.f.	Mean Square	
		4 days after inoculation	6 days after inoculation
Locations	1	1.77 *	11.40 ***
Males	9	1.75 ***	2.28 ***
Female/Males	30	0.52	0.74
Males × Locations	9	0.29	0.25
Females/Males × Locations	30	0.36	0.42
Coefficient of variation (%)		14.66	14.16
Mean		4.11	4.60
Narrow sense heritability		0.78	0.74

* and *** indicate significance at the 0.05 and 0.001 levels.

Table 5. General combining ability estimates (g_i) and slopes (as measured by the coefficient of regression, b) for early blight development of each parental clone used in the 6 × 6 diallel.

Parental clone	g_i	$b + S_b$
381328.18 (S)	0.05	0.030 + 0.002
381348.7 (S)	0.20 *	0.040 + 0.000
FH-122 (R)	− 0.10	0.020 + 0.004
FH-92 (S)	0.04	0.023 + 0.002
MI-49.10 (S)	0.19 *	0.033 + 0.004
MI-17.12	− 0.37 *	0.017 + 0.002
standard error (g_i)	0.08	
standard error for GCA comparison ($g_i - g'_i$)	0.12	

(S) and (R) indicate that the parent was either susceptible or resistant to early blight.

* indicates a g_i value significant larger than zero.

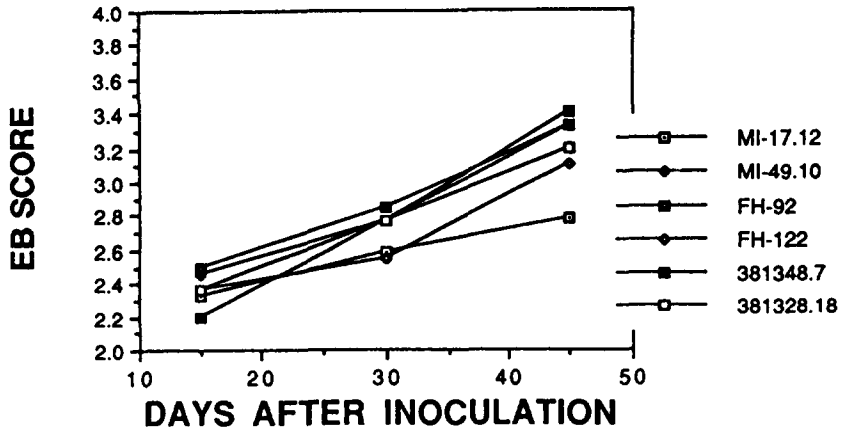

Fig. 1. Early blight development in diploid progenies of potato. Results were grouped according to parental clone (San Ramon, 1987).

example, the clone 381348.7 was one of the best parents under controlled conditions and in the early field evaluation but had the highest early blight susceptibility score in the last evaluation. This resulted in its high regression coefficient for disease development. Therefore, this may explain why Martin et al. (1986) indicated that results of early screening for the disease under controlled conditions were not significantly correlated with field resistance of the same materials.

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