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Genetic foci of *Solanum* species, *Petota* Dumort, resistant to *Phytophthora infestans* (Mont.) De Bary

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Abstract

The present paper provides a review of data from literature sources and results of research carried out at the Institute of Plant Industry with the aim of identifying genetic centres of formation of late blight resistant genotypes. For the research results, species from the potato collection of VIR were used.

Introduction

In his fundamental work 'Centers of origin of cultivated plants' Vavilov (1926) noted that the centre of potato type-formation embraces the mountainous regions of Mexico, Guatemala, Colombia, Peru and the adjacent regions. The foci of *Solanum* resistance genes were considered to be in these areas (Vavilov 1964).

Niederhauser et al. (1954) reported *Phytophthora infestans* to be widely spread within wild potato species in central Mexico. This disease was destroying plants of the species that did not possess genes of resistance to this pathogen. For the same reason, Zhukovsky (1954) stated that, the potatoes introduced in Mexico from Chile all died from late blight. An example of the linked evolution of both the host and pathogen in their common native country (in Mexico) is the relationship between the wild tuberiferous potato species and late blight which forms here a multitude of races and biotypes. Different levels of late blight resistance are attributed to the same potato species by different scientists. For instance, Kameraz (1959) believes that *S. bulbocastanum* was not susceptible to late blight either in the field or with artificial inoculation of their leaves. On their part, Rudorf and Schaper (1951) share an opinion that samples of this species manifest varying degrees of resistance.

Niederhauser et al. (1954) noted that inoculation with the most aggressive races of late blight in the Toluca region, of Mexico, revealed only one clone of *S. bulbocastanum* that remained unaffected. According to Wriedt (1955), only some clones of *S. stoloniferum* and one clone of *S. verrucosum* were not susceptible to late blight. In compliance with the data from Kameraz (1959), all the tested samples of *S. verrucosum* were resistant to common races in field conditions, but became infected by more aggressive biotypes.

The above contradictory evaluations corroborate our conclusions about the non-uniformity of *S. verrucosum* in terms of its genotypic resistance to late blight Budin (1986, 1987, 1992), Budin and Gavrilenko (1994), Budin and Soboleva (1987), Kameraz (1959), Zoteyeva (1986). Many scientists and breeders, however, still regard this entire species as resistant and do not subject the forms involved in crosses to preliminary evaluation for late blight resistance.

This, probably, may explain why no significant success has been achieved during 70 years of breeding for late blight resistance (Ross 1984).

In this regard, large potato genebanks (Hanneman and Bamberg (1986), Budin and Soboleva (1987), Van Soest et al. (1984)) independently carried out in the 1980s evaluation of late blight resistance in a great number of genotypes (600–700) of 35 species introduced into their collections. The results of our research are presented in this paper.

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Results and comments

The screening of 15 Mexican wild potato species revealed genotypic polymorphism in the level of resistance to late blight (resistant, medium resistant, non-resistant).

Out of 183 genotypes (Table 1), 90 late blight resistant collections were selected, including genotypes of *S. pinnatisectum*, *S. brachycarpum* and *S. trifidum* which are all resistant to late blight. They do not cross with other species and do not produce berries from self-pollination. The area of distribution of these species is not large and is located in the same phyto-geographical conditions between 20–21N and 100–103W (Figure 1, Hawkes (1966)) at altitudes between 1600 and 2000 m. Resistant genotypes (63–66% of total genotypes) of *S. bulbocastanum* and *S. demissum* occur within the area located between 19–21N and 98–99W at altitudes from 2000 through 2700 m. The medium-resistant and the non-resistant types of these species occur in the region within 22–30N and 16–17N, 98–100W, at altitudes from 1500 to 3000 m where conditions are not favourable for the development of late blight.

Other species' areas of distribution (Figure 2, Hawkes (1966)) are located in central and northern Mexico at 18–21N and 22–31N, respectively. For the latter region, deserts and semi-deserts with xerophytic vegetation, dry continental climate and conditions unfavourable for late blight development are characteristic.

As a result, among the 15 Mexican wild potato species studied, 86 genotypes of 9 species (46.9%) were found to be late blight resistant.

341 genotypes of 20 species introduced into collections of the above-mentioned genebanks from South America were studied. All in all, 62 late blight resistant genotypes belonging to 8 species were identified. Forty-six genotypes originate from Colombia and Ecuador, 5 from Bolivia, and 11 were found among wild potato species from Argentina.

In Colombia and Ecuador resistant forms were found within the species *S. phureja*, *S. tuberosum* ssp. *andigena*, *S. andreanum*. They occur in the departments of Narino, Cauca and Imbabura, having geographical coordinates 00.54–01.19N–76–77W at altitudes ranging from 2700 to 3000 m (Table 2).

In Bolivia, *S. berthaultii* and *S. toralapanum* were found to have resistant genotypes in the Cochabamba and Chuquisaca departments (17S–60W, at altitudes from 2500 to 2700 m) (Table 3).

In Argentina, the late blight resistant genotypes

Table 1. Race non-specific late blight resistance of Mexican wild *Solanum* species. Data from 3 genebanks.

Species	Genebank/Country	Genotypes studied				Geographical data on resistant genotypes		
		Total	Percentage of					
			resistant	medium resistant	non-resistant	Latitude (N)	Longitude (W)	Altitude (m)
S. pinnatisectum	USA	12	100	0	0	20–21	100–103	1600–2000
	Russia	11	100	0	0			
	Germany-Netherlands	17	94	6	0			
S. bulbocastanum	USA	23	63	22	15	17–21	98–100	1500–2400
	Russia	14	86	7	7			
	Germany-Netherlands	13	92	8	0			
S. demissum	USA	70	66	30	4	19–20	98–99	2600–3000
	Russia	30	66	17	17			
	Germany-Netherlands	54	66	30	4			
S. stoloniferum	USA	45	58	12	30	16–21	98–102	2200–2400
	Russia	8	70	25	5			
	Germany-Netherlands	4	75	25	0			
S. polyadenium	USA	10	50	50	0	19–21	97–101	2000–2500
	Russia	21	53	33	14			
	Germany-Netherlands	9	90	10	0			
S. verrucosum	USA	15	46	26	28	19–21	98–102	2100–2600
	Russia	15	40	40	20			
	Germany-Netherlands	14	43	40	17			
S. cardiophyllum	USA	5	15	45	40	20–21	99–102	1600–2200
	Russia	13	12	44	44			
S. brachycarpum	USA	2	100	0	0	19	100	2400
	Germany-Netherlands	1	100	0	0			
S. trifidum	USA	3	100	-0-	-0-	19	102	2200–2300

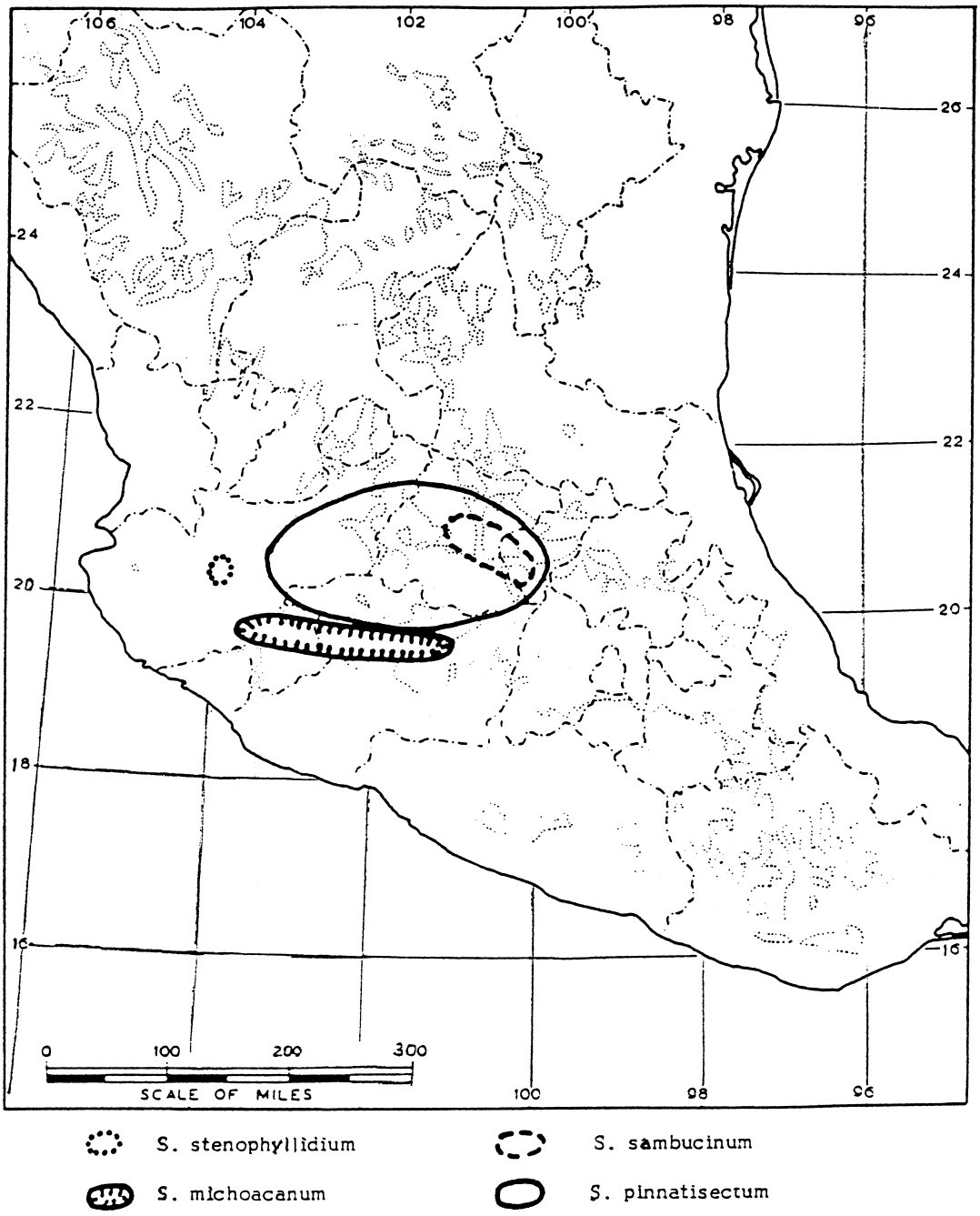

Figure 1. Areas of distribution (according to Hawkes) of the species entirely resistant to late blight.

were identified within the species *S. microdontum*, *S. vernei*, *S. tarijense*. These were collected in the Salta and Jujuy departments (22–25S–64–65W, altitudes from 1500 through 2900 m) (Table 4).

It follows from the above that in the South American countries mentioned the genotypes resistant to late blight comprise 18% of the total genotypes studied, i.e. approximately 2.6 times less than in Mexico where this figure is 46.9%. The species non-resistant to late blight (Table 3,4) grow either in valleys at low altitude ranging from 50 to 1000 m and at high temperature (40–50 °C), or high in the moun-

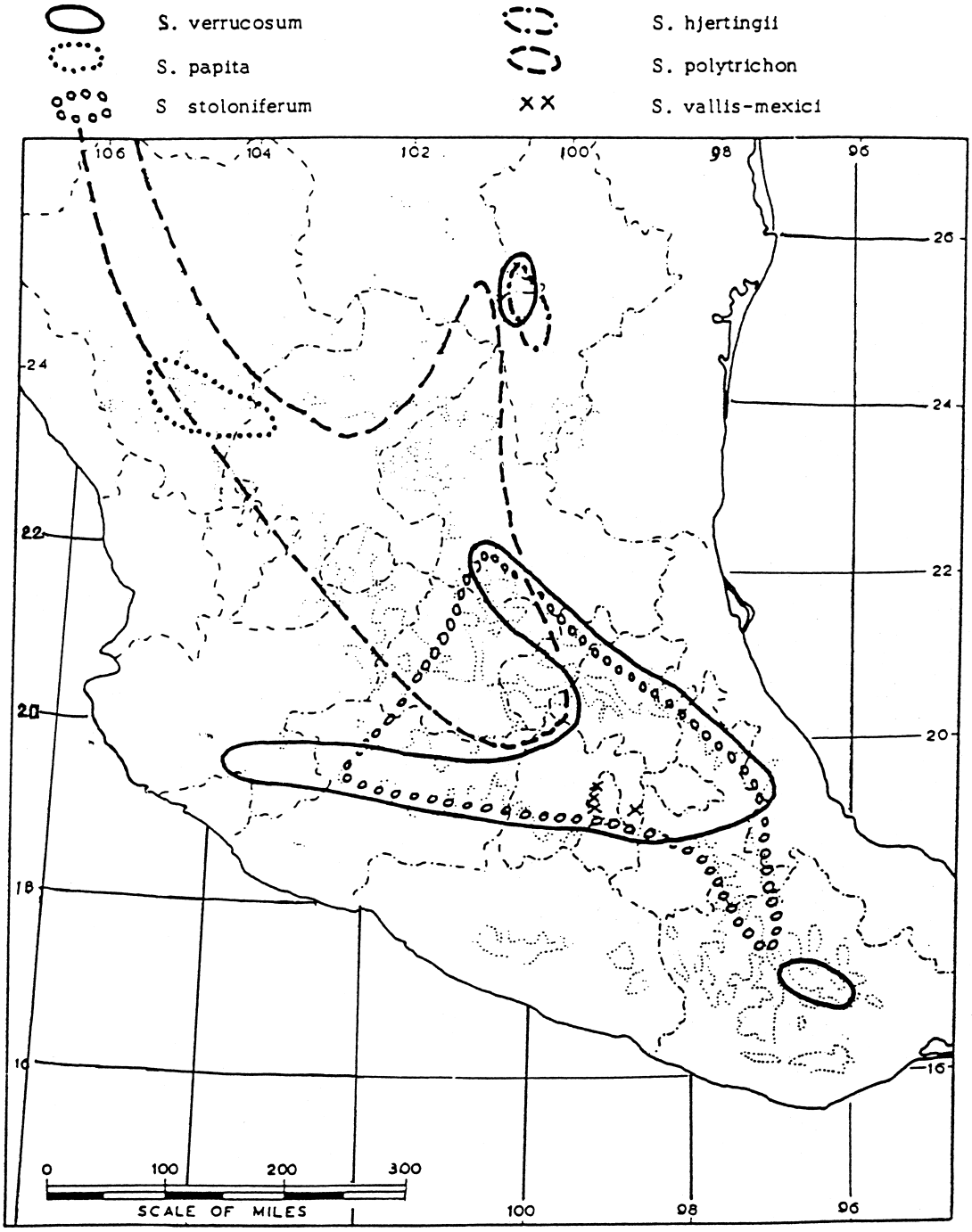

Figure 2. Areas of distribution (according to Hawkes) of the species possessing genotypes resistant and non-resistant to late blight.

Table 2. Race non-specific late blight resistance of *Solanum* species from Colombia and Ecuador.

Species	Genebank/Country	Genotypes studied				Geographical data on resistant genotypes		
		Total	Percentage of					
			resistant	medium resistant	non-resistant	Latitude (N)	Longitude (W)	Altitude (m)
S. phureja	USA	52	57	25	18	00.54–	76–77	2700–3000
	Russia	13	23	7	70	01.13		
	Germany-Netherlands	18	0	0	100			
S. tuberosum	USA	210	9	10	81	01.05–	77	2700–3000
ssp. *andigena*	Russia	12	32	18	50	01.13		
	Germany-Netherlands	197	0	45	55			
S. andigenum	USA	2	50	50	0	01.19	77	2900

tains at elevations from 3000 to 4500 m where the temperature drops below 0 °C at night. In both cases, late blight cannot develop under the given conditions.

Genetic foci of formation of the late blight resistant potato species

On the basis of the available phyto-geographical data and results of searches for resistant genotypes of the species introduced in the collections, it is possible to define 4 genetic centres of formation of potato species possessing resistance to late blight.

The Mexican gene centre includes a narrow strip between the Pacific and the Gulf of Mexico in the Atlantic (Figure 3) areas in southern Mexico between 18–21N–98–101W at altitudes from 1900 to 3100 m, and in the states Mexico, Distrito Federal, Michoacan, Morelos, Pueblo, Hidalgo, Veracruz, Oaxaca, Guanajuato and Jalisco. This is a mountainous area with mountains and volcanos, and with evergreen forests, shrubs and grasses growing on the slopes and in the valleys. The average temperature is from 13 to 18 °C, and the maximum values range from 14 to 21 °C. Precipitations of 568 to 807 mm occurs mainly in the summer; the air humidity is 77%. All this ensures ideal phyto-geographical and phyto-climatic conditions for the development of the fungus *Phytophthora infestans* and wild potato species.

In the Mexican centre, sexual reproduction of *P. infestans* takes place *in vivo* and the environment is ideal for the development of late blight. As a consequence, intensive pressure of natural selection leads to the development within the species of resistant forms which should be used by breeders as sources in breeding for late blight resistance.

In South America 3 gene centres of formation of late blight resistant genotypes have been defined.

The Colombian-Ecuadorean gene centre is located between the rivers Cauca and Magdaleña, between central and eastern Cordilleras, at altitudes from 2200 to 2900 m in the departments of Narino and Cauca (00.54–01.13N 76–77W) in Colombia, and in the Imbabura department in Ecuador (00.18S 78W). The centre stretches for 250 to 300 km from northern Ecuador to southern Colombia.

Climatic conditions are moderately warm with temperatures from 14 to 21 °C, air humidity of 73% and 400 to 700 mm of rainfall. These conditions are

Table 3. Race non-specific late blight resistance of *Solanum* species from Bolivia.

Species	Genebank/Country	Genotypes studied				Geographical data on resistant genotypes		
		Total	Percentage of					
			resistant	medium resistant	non-resistant	Latitude (S)	Longitude (W)	Altitude (m)
S. berthaultii	USA	4	75	25	0	17	61	2500–2700
	Russia	9	44	56	0			
	Germany-Netherlands	11	64	30	6			
S. toralapanum	USA	4	25	0	75			
	Germany-Netherlands	12	0	69	31			
S. sparsipilum	USA	6	0	0	100	17	66	2500–3000
	Russia	20	0	25	75			
	Germany-Netherlands	26	3	32	65			
S. boliviense	USA	5	0	0	100	19	65	2700–3600
	Germany-Netherlands	10	10	20	70			
S. leptophyes	USA	1	0	0	100	19	66	3500–3700
	Germany-Netherlands	28	0	17	83			

Table 4. Race non-specific late blight resistance of *Solanum* species from Argentina.

Species	Genebank/Country	Genotypes studied				Geographical data on resistant genotypes		
		Total	Percentage of					
			resistant	medium resistant	non-resistant	Latitude (S)	Longitude (W)	Altitude (m)
S. microdontum	USA	15	26	46	28	22–25	64–65	1500–3500
	Russia	18	28	16	56			
	Germany-Netherlands	32	60	30	10			
S. vernei	USA	7	0	56	44	23–25	64–65	2400–3400
	Russia	21	24	40	36			
	Germany-Netherlands	24	40	30	30			
S. tarijense	USA	6	0	0	100	22–25	64–65	2150–2900
	Russia	14	7	80	13			
	Germany-Netherlands	14	14	30	56			
S. spegazzinii	USA	11	0	36	64	24–28	65–67	1400–3200
	Russia	28	0	10	90			
	Germany-Netherlands	38	5	16	79			
S. chacoense	USA	25	0	12	88	23–32	64–67	600–2700
	Germany-Netherlands	68	4	20	76			
S. kurtzianum	USA	5	0	0	100	27–33	66–67	900–2500
	Germany-Netherlands	10	0	0	100			
S. megistacrolobum	USA	9	0	0	100	22–25	65–66	3400–4200
	Germany-Netherlands	40	0	5	95			
S. sanctae-rosae	USA	5	0	16	84	26	66–68	2900–3500
	Germany-Netherlands	9	0	0	100			
S. acaule	USA	21	0	9	91	21–23	65–67	3000–4200
	Germany-Netherlands	87	0	45	55			
S. commersonii	USA	4	0	25	75	30–36	56–58	50–150
	Germany-Netherlands	5	0	20	80			

favourable for the development of potato plants of the host species and the parasite, *Phytophthora infestans*.

This centre features late blight resistant genotypes of such species as *S. phureja*, *S. tuberosum* ssp. andigena and *S. andreanum*.

The Bolivian gene centre embraces the departments of Cochabamba and Chuquisaca in the central part of the country, on the eastern slopes of the Andes (2500–2700 m, 17–19S 65–77W). Climatic conditions favour the development of late blight: average temperatures are 15 to 19 °C, air humidity is 75%, and rainfall varies from 562 to 665 mm. Here a centre of late blight resistant forms of *S. berthaultii* and *S. toralapanum* is situated. Within these species, late blight resistant genotypes have been found among shrubs, on sandy slopes, on side roads, among rocks in the mountains, and on the edges of mountainous slopes and precipices.

The Argentinian centre embraces the large Tilcara valley stretching along the river, the foothills of the northeastern part of the country, and Salta and Jujuy provinces (22–25S 64–65W, altitudes from 1500 to 3000 m). The centre is located on the eastern slopes of the Andes with subtropical forests, shrubs, mountain plateaux and cultivated fields. The climate here is moderately humid (75% humidity, 722–929 mm rainfall) and moderately warm (19–22 °C). Such species as *S. vernei*, *S. microdontum* and *S. tarijense* have been introduced into collections from here and found to contain late blight resistant genotypes.

In these centres in the area of origin of both the host and the pathogen the joint evolution of potato species and the fungus *Phytophthora infestans* is ongoing. In the course of the evolution, changes in gene combinations and mutations occur and cause in the host transformations in its mechanisms of resistance which later become fixed through selection, and in the pathogen they determine changes in the aggression mechanisms. That is how the dynamic equilibrium between the host and the pathogen was evolving to determine the interaction of mutation and selection within the host and the pathogen.

All the genetic foci are located at a corresponding geographical latitude and longitude at similar altitudes from 1500 to 2900 m. Obviously, phyto-climatic conditions that form at these altitudes in Central and South America are favourable for the development of *Phytophthora infestans*. This fungus is known to exist at temperatures from +3 °C to +28 °C and humidity of no less than 75%. Such conditions (C and S.

America) form in the mountains with evergreen or deciduous forests and shrubs, and favourable temperature and high humidity.

Summary

A significant rate of polymorphism differentiates potato species. Among a large number of genotypes, forms showing high resistance, medium resistance and susceptibility to late blight have been found.

The highly-resistant genotypes form in gene centres where they exist together with late blight in their common area of origin.

The paper mentions 4 gene centres from which 17 species have been selected and found to contain 173 genotypes resistant to the pathogen.

The highest genetic potential has been demonstrated by such species as *S. bulbocastanum*, *S. demissum*, *S. stoloniferum*, *S. pinnatisectum*, *S. polyadenium*, *S. berthaultii*, *S. microdontum* and *S. trifidum*. (Table 5)

It would be reasonable to continue studies of the species which have already been found to possess late blight resistant genotypes, as well as the species occurring in the areas adjacent to the gene centres.

All attempts to search for late blight resistant forms within the species occurring in valleys, at elevations up to 1200 m and in the mountains at altitudes above 300 m will be futile.

Table 5. Late blight resistant genotypes of *Solanum* species and their gene centre.

Species	Number of genotypes	Genetic focus
S. pinnatisectum	12	Mexican
S. bulbocastanum	14	Mexican
S. demissum	39	Mexican
S. stoloniferum	26	Mexican
S. polyadenium	5	Mexican
S. verrucosum	7	Mexican
S. brachycarpum	2	Mexican
S. trifidum	3	Mexican
S. cardiophyllum	2	Mexican
S. phureja	29	Colombian-Ecuadorean
S. tuberosum ssp. *andigena*	19	Colombian-Ecuadorean
S. andreanum	1	Colombian-Ecuadorean
S. berthaultii	3	Bolivian
S. toralapanum	1	Bolivian
S. microdontum	4	Argentinian
S. vernei	5	Argentinian
S. tarijense	1	Argentinian

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