*Potato Research 33 (1990) 341–347*

# Wild tuber-bearing species of *Solanum* and incidence of *Phytophthora infestans* (Mont.) de Bary on the Western slopes of the volcano Nevado de Toluca. 2. Distribution of *Phytophthora infestans*

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Accepted for publication: 22 March 1989

*Additional key words:* late blight, *Solanum demissum*, *S. verrucosum*, altitude

## Summary

An area of 15 000 ha on the Western slopes of the volcano Nevado de Toluca was surveyed during 1982–1986. The occurrence of late blight (*Phytophthora infestans*) was studied in 1986 along five long (7–10 km) transects from an altitude of 2900 m to 3900 m, the upper limit of *Solanum demissum (dms)* and in all years in some other sites. Late blight was confined to scattered pockets, 100–500 m in diameter, separated by several kilometers. In 789 colonies of wild *Solanum* spp., each consisting of 4 to >100 plants per colony of *dms, verrucosum (ver), iopetalum, brachycarpum,* × *edinense, stoloniferum* or one unidentified species, symptoms were found in 10 % of the colonies or less than 1 % of the plants in each colony. Plants had few (1-2) lesions which did not affect vigour. No infected tubers were found. Most (64 %) of the infected colonies were of *dms*, the predominant species (69 %). Colonies of *ver* were less frequent (11 %) and 17 % were infected. No infected plants were found in the unidentified species, thought to be *dms* × *ver*.

## Introduction

Mexico is regarded as the centre of diversity of the fungus *Phytophthora infestans* (Mont.) de Bary, the cause of late blight in potatoes. Each year the disease is present in the Toluca Valley (Mills & Niederhauser, 1953) and widespread in the central Mexican highlands (Niederhauser et al., 1954) and until recently its two comptability types, A1 and A2, were known to occur only in Mexico (Gallegly & Galindo, 1958; Galindo & Gallegly, 1960). In the *Solanum* species indigenous to Mexico, a complex of resistance genes is assumed to have evolved through natural selection (Toxopeus, 1964). Mexican wild tuber-bearing species of *Solanum* (WSS), especially *Solanum demissum* (*dms*), have been widely used as sources of both race-specific and general resistance to late blight in potatoes (Niederhauser & Mills, 1953; Rowe, 1969; Howard, 1970; Umaerus, 1970; Umaerus et al., 1983).

It is not known to what extent and by which mechanisms Mexican WSS are protected from *P. infestans* in their natural habitats. Rivera-Peña & Molina Galan (1989) have described the occurrence and distribution of WSS in the area under investigation (see below), selected as being close to the Toluca Valley and still little disturbed by human activities. This paper presents the results of a survey of the occurrence and distribution of *P. infestans*.

## Materials and methods

The investigation was carried out in an area of 15000 ha on the western slopes of the volcano Nevado de Toluca in the state of Mexico. A map and description of the area, and data concerning WSS, other vegetation, temperature and precipitation have been given by Rivera-Peña & Molina Galan (1989).

The study was initiated in 1982 in San Juan de las Huertas (SAJ) along a 500 m-long transect at an altitude of 2900-3000 m. This area, which was influenced by cultivation, was surveyed annually until 1986. In 1983 and 1984 a site at Tenango (T), located on the eastern slopes, was also studied, and in 1984 other sites were included: San Pedro Techuchulco (SP) on the eastern slope and Loma Alta (LA), Mezon Viejo (MEZ), Raices (RA), K-12, K-14, K-18 and Forestal (F) on the western slope. In 1985 five long (7-10 km) transects covering altitudes from 2900 to 3900 m were visited once during the period mid-August to early October. In addition, detailed observations were made and samples of all infected plants were collected along short (300-500 m) transects at SAJ, La Puerta (PUR), LA, MEZ, La Penuela (PEN), RA, K-12, K-14, Las Lagrimas (LAA), Yecapixtla (YEC) and La Joya (JOY) and nine short (300 m) transects at F. Six sites (SAJ, RA, F, JOY, MEZ and LA) were visited every 10 days from March to October, 1986.

Cultivated potatoes, including cv. Lopez which was used as a susceptibility check (r), were present in SAJ (long transect 4; 2950 m), PEN (transect 1; 2900 m), and MEZ (near transect 1; 2700 m) and this cultivar was planted at RA (transect 1; 3500 m), F (transect 2; 3300 m) and JOY (transect 5; 3000 m).

The development of late blight was observed in all years at the Toluca (TOL) Experimental Station, 2600 m, where much of the breeding material possessed R-genes. All plants in most WSS colonies along the short transects, and colonies at 100 m intervals of altitude along the long transects, were also examined for disease symptoms. Samples were taken from all plants with foliage symptoms suspected to be caused by *P. infestans* and examined microscopically after incubation for 24 h in plastic bags kept at room temperature. Tubers were likewise incubated, but for three days prior to inspection.

## Results

Late blight did not occur consistently (Table 1) and of 789 colonies of WSS observed over all the years 1982-1986, infection by *P. infestans* was confirmed in 81 (10.3 %, Table 2) but usually only on one plant in each colony. Colonies comprised between 4 and several hundred plants (Rivera-Peña & Molina Galan, 1989), with an average of 11 and a density of 2-120 per square metre. However, there may have been an overestimate of the incidence of infection because some sites were chosen where *P. infestans* was known or thought to be frequent. Observations along the long transects in 1985, covering altitudes between 2900 m and the upper limit of WSS distribution, provided a more reliable estimate of overall infection frequency in the area; late blight was found in 12 (6 %) of 189 colonnies (Table 3).

Table 1. Occurrence of late blight infection at different altitudes 1982 – 1986.

| Site[a] | Altitude m | 1982 | 1983 | 1984 | 1985 | 1986 |
|---|---|---|---|---|---|---|
| | 3900 | | | | 0 | |
| | 3800 | | | | 0 | 0 |
| | 3700 | | | | 0 | 0 |
| | 3600 | | | | 0 | 0 |
| RA | 3500 | | | 0 | + | + |
| K-12 | 3500 | | | 0 | | |
| K-14 | 3450 | | | 0 | | |
| F | 3300 | | | + | + | + |
| LA | 3270 | | | 0 | | 0 |
| K-18 | 3250 | | | 0 | | |
| LAA | 3110 | | | | 0 | 0 |
| SAJ | 3000 | 0 | + | + | + | + |
| JOY | 3000 | | | | + | + |
| PEN | 3000 | | | | + | 0 |
| POT | 2900 | | | | | + |
| YEC | 2800 | | | | + | |
| MEZ | 2700 | | | + | + | + |
| T | 2600 | | + | 0 | 0 | |
| TOL | 2600 | + | + | + | + | + |

[a] for site abbreviations, see text.
+/0 = *P. infestans* found/not found.

Table 2. Incidence of late blight in wild *Solanum* species (WSS) 1982 – 1986.

| Species | Colonies | | | | |
|---|---|---|---|---|---|
| | inspected | | infected | | |
| | No. | % of WSS | No. | % | % of WSS |
| *S. demissum (dms)* | 543 | 69 | 52 | 9.6 | 64.2 |
| *S. verrucosum (ver)* | 88 | 11 | 15 | 17.0 | 18.5 |
| *S. iopetalum (iop)* | 31 | 4 | 2 | 6.4 | 2.5 |
| *S. brachycarpum (bra)* | 30 | 4 | 7 | 23.3 | 8.6 |
| *S.* x *edinense (edn)* | 24 | 3 | 2 | 8.3 | 2.5 |
| *S. stoloniferum (sto)* | 31 | 4 | 3 | 8.1 | 3.7 |
| Unidentified species | 42 | 5 | 0 | 0.0 | 0.0 |
| Total | 789 | 100 | 81 | 10.3 | 100.0 |

Late blight was not found in WSS along three of the transects (Nos. 2, 3 and 4), although *P. infestans* was present in the susceptible cv. Lopez (r) in transects 2 and 4. Also, none was seen above 3500 m (Table 1) although *dms* grew to an altitude of about 3900 m (Rivera-Peña & Molina Galan, 1989).

Table 3. Incidence of late blight infection in wild *Solanum* species along five long transects 1985.

| Species[a] | Colonies | | | | |
|---|---|---|---|---|---|
| | inspected | | infected | | |
| | No. | % of WSS[a] | No. | % | % of WSS |
| *dms* | 140 | 74 | 7 | 5 | 58 |
| *ver* | 8 | 4 | 1 | 12 | 8 |
| *iop* | 17 | 9 | 2 | 12 | 17 |
| *bra* | 16 | 9 | 2 | 12 | 17 |
| *edn* | 8 | 4 | 0 | 0 | 0 |
| *sto* | 0 | 0 | - | - | |
| unidentified species | 0 | 0 | - | - | |
| Total | 189 | 100 | 12 | 6 | 100 |

[a] abbreviations as in Table 2.

No symptoms of *P. infestans* were found on tubers of WSS collected up to the middle of October from plants with foliage symptoms.

Late blight was found in all WSS growing in the area except on the unidentified species (*unsp*), thought to be a hybrid between *dms* and *S. verrucosum* (*ver*), which was found in a limited area at Forestal (Rivera-Peña & Molina Galan, 1989).

*Dms* was the most frequent WSS (69 %) in the area and 64 % of the colonies with late blight were of this species (Table 2). However, proportionately more lesions (17 %) were found on *ver* which made up 11 % of the total population of WSS, Few colonies of other *Solanum* spp., (*iopetalum, brachycarpum* (*bra*), × *edinense* (*edn*), *stoloniferum* (*sto*)) were found although in all species a small proportion of plants were infected.

At the Experimental Station in the Toluca Valley (TOL), late blight was found on *S. tuberosum* and on breeding material from early July until late October in every year; in 1986 lesions had already appared in late June and severe attacks were also seen in cultivated areas within and adjacent to the survey area where cv. Lopez (r) was grown.

The position and number of WSS colonies changed little between years but the frequency of infection, the position of infected colonies along the transect, and the species infected varied between years, as did the time when the first lesions were seen. In 1982, late blight was not found in WSS in SAJ during 11 visits made between July 10 and October 26 and covering an area of 5000 $m^2$ although infections were seen in cultivated potatoes. In August, late blight was found on one plant of *edn* in 1988 and on one of *sto* in 1984. On July 5, 1985, it was seen on plants of both *sto* and *dms* and it was still evident in October. In 1986, the SAJ area was visited at ten day intervals; by 5 June infection was found on cv. Alpha and on 25 June among colonies of *dms*. Thereafter it was found on the other two WSS (*sto, edn*) in the area and infected plants of *dms* were still found in October.

Late blight was detected at F (3300 m) in all three years in which observations were made (Table 1). The distribution of infected colonies was studied in 1985 in the nine short transects covering this area, where four WSS grew. They are more abundant in this than in other areas and colonies often comprised more than one species. Infected plants of *dms, ver*, and *bra*, but never of *unsp*, were found in all years. The first lesions were found in August 1984, in July 1985 and in *dms* in June 1986. Lesions were still present in October 1985.

Late blight was not found among *dms, ver*, and *bra* colonies at RA in 1984, but in 1985 and 1986 infection was evident on *ver* and *bra*. This was the highest altitude (3500 m) at which infected plants were found. Late blight was seen in 1985 only on *ver* at the beginning of August but in 1986 infections were seen on *ver* at the end of June and later, also, on *bra*. Only 9 infected colonies of WSS were infected of about 200 that were inspected. The cv. Lopez was planted in RA in 1986 and was infected by the end of June.

During the period 1982-86, 81 colonies of WSS were found with late blight of which 76 had infection only on leaves, whereas stem infections were present on only 5 plants. There was no clear difference in lesion distribution between species.

Lesions occurred with similar frequencies in the top (26), middle (29) and lower (26) regions of 81 plants although the earliest lesions seen (57 %) were often on the lower leaves in contact with soil. Some of these lower lesions may have escaped detection.

Sequential observations on infected plants showed that lesions usually dried without increasing in size or sporulating so that infected leaves survived and the plant appeared healthy. Occasionally, when environmental conditions favoured fungal growth, lesions started to expand again.

## Discussion

The environment in the Toluca Valley is considered to be one of the most favourable in the world for the development of late blight infection in potatoes (Niederhauser & Mills, 1953). Reddick (1932) made habitat observations on *Solanum* species and *P. infestans* in the Federal District near Desierto de los Leones as did Niederhauser & Mills (1953) on the slopes of the volcano Popocatepetl but these authors did not give information on the frequency of late blight.

In our survey, attacks of late blight were much less severe than expected. In the first year of observations late blight was not found and during five years only 10 % of the wild *Solanum* colonies examined were found to be infected. Moreover, the symptoms were so mild that it was unlikely that any plant would have been prevented from producing tubers. However, it is possible that some young plants could have been killed soon after emergence and, therefore, were not recorded.

Niederhauser et al. (1954) concluded that race-specific resistance to late blight does not provide sufficient protection under Mexican conditions and we therefore assumed that WSS are protected from eradication by a high level of non-specific resistance, an assumption based on work in the experimental fields in the Toluca valley.

There may be reasons other than resistance that account for the low frequencies of infection in the natural habitat. The area chosen may not have been as representative of the Toluca Valley as expected and infection may have been scarce because of low initial inoculum; the environment too may have been less conducive to infection than expected and, wide spacing between colonies and heterogeneity of the natural vegetation may have reduced infection frequency.

Epidemics of late blight usually start in susceptible cultivars (Van der Zaag, 1959) and symptoms in WSS were usually not found until about two months later. This observation may indicate that disease resistance was important.

The origin of inoculum was not detected and although mycelium overwintering in tubers is thought to be the most important source for initiating epidemics (Hirst, 1955), infected tubers of WSS were not found. Lapwood (1971) suggested that epidemics in the Toluca Valley originated from stems infected at soil level by soil-borne *P. infestans*. As the first lesions recorded were often on leaves in contact with soil, it might suggest that oospores were involved in the initial infections. Environmental conditions in the area are favourable for oospore formation (Romero & Erwin, 1967; Gough et al., 1957; Smoot et al., 1958) and Gallegly & Galindo (1958) observed oospores in lesions on leaves collected on the volcano Popocatepetl on 7 August.

Some of the areas surveyed were exposed and so liable to drying and, consequently, when sporangia were released it is unlikely that they would survive (Makela, 1966). However, the uneven distribution of late blight may partly be explained by the effects of humidity because early attacks and large numbers of plants with lesions were found in all WSS in localised areas characterized by high humidity and luxurious plant growth. Such areas were observed in F and JOY and could be expected to provide a continuous supply of inoculum.

Low temperatures probably limit late blight development at high altitudes and none was found above 3500 m, although the susceptible *S. demissum* was present up to 400 m higher. However, at this altitude it is unlikely that inoculum or humidity were limiting factors because rain and fog are frequent and clouds moving up the slopes may carry inoculum. Night temperatures above 3500 m are often as low as +5 °C and, occasionally, frost occurs.

Most investigations on *P. infestans* have been made where vegetation is more uniform than in the area surveyed. Non-*Solanum* vegetation may have hindered dispersal of *P. infestans* and the large distances between susceptible plants delayed development of epidemics. In open areas, *dms* plants were stunted rosettes, providing small targets for inoculum although dense stands of fir and pine forest create suitable humid microenvironments. Distances between colonies were often large and it may be that they escaped infection because inoculum had been diluted to amounts below the threshold necessary for infection. However, lesions were usually found on susceptible *S. tuberosum* (r), wherever it was cultivated in the neighbourhood, suggesting that resistance was present in the wild *Solanum* species.

## Acknowledgements

The author thanks Professors Magnhild Umaerus and Vilhelm Umaerus for valuable discussions and revision of the manuscript.

Support from the following sources is gratefully acknowledged: financial support and working facilities provided by Instituto Nacional de Investigaciones Forestales y Agropecuarias, programa de papa, in Mexico; financial support provided by the Swedish Institute during my stay in Uppsala.

The linguistic revision of the manuscript by David Tilles is acknowledged.

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