Potato multiple virus resistant potatoes in Peru

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Abstract
The potato is highly susceptible to virus diseases that may drastically reduce tuber yield and quality being PVX, PVY and PLRV the primary causal agents of the “crop degeneration” that gradually reduces yield. Farmers of developed countries use certified seed to avoid virus damage even planting susceptible cultivars. In the developing world where quality seed is expensive, scarce or unavailable, virus resistance is the only way to control virus damage.

Immunities to PVX and PVY are simply inherited at independent loci with dominant immunity alleles. PLRV infection resistance despite of its polygenic control has a sizable additive gene action and medium-high heritability that ensures a good response to selection.

Breeding multiple virus resistant potatoes started at the International Potato Center (CIP) in the 1980’s. As a result triplex progenitors, XXXxYYYy, were assembled being important for transmitting immunity to both viruses to 96.4% of its progenies when crossed to any susceptible multiplex genotype, xxxxyyyy.

High yielding PVX and PVY immune progenitors crossed with PLRV resistant sources produced multiple virus resistant materials from which early maturing, high yielding and good tuber quality new cultivars are grown in Peru and African and Asian countries.

Keywords: Potatoes, Breeding and genetics, Virus resistance, Combining ability.

Introduction
The potato, *Solanum tuberosum* L. has many enemies: 23 viruses, 38 fungi, 6 bacteria and 1 viroid. From these, the most damaging are *Phytophthora infestans* causing late blight and leaf roll (PLRV), Y (PVY) and X (PVX) viruses, main agents of “potato degeneration” causing a gradual weakening of plants and reducing tuber yield and quality as infection rate increases with time. Vegetative propagation enhances virus spread in time and space as infected seed tubers carry disease from one season to the next and from one field to another.

Farmers of developed countries avoid virus disease damage using certified seed tubers that frequently renewed permits planting susceptible cultivars. However, in most developing countries certified seed could be too expensive, scarce or unavailable forcing farmers to often use infected seed. In this scenario, the only effective control of “degeneration” is the use of virus resistant cultivars. Otherwise, reduction of tuber yield and quality might be significant.

This paper reports the virus resistance breeding developed at CIP from 1982 to 1997 emphasizing its genetic aspects, philosophy and pragmatic strategy, genetic resources utilized and its outputs as new varieties released in Peru and other countries (Mendoza et al. 1989).

Genetic aspects of virus resistance
PVX and PVY immunities are controlled by single loci with complete dominance. At the PVY locus the allele Y controls immunity and y, susceptibility and segregate under a random chromatid model, $\alpha = 1/7$ (Mendoza et al., 1996). At the PVX locus X controls immunity and x, susceptibility, under a random chromosome model, $\alpha = 0$ (Mendoza et al., 2008a).
In addition, at an autotetraploid single locus several genotypes are possible, i.e., quadruplex (YYYY), triplex (YYYY), duplex (XXxx), simplex (Yyyy) and nulliplex (yyyy). Since PVY and PVX immunities are dominant, the presence of a single Y and X alleles will confer immunity to both viruses. However, their parental value is significantly different when crossed to any susceptible clone, xxxxyyyy. A simplex XxxxYyyy produces 25% of progenies immune to PVX and PVY, a duplex XXxxYYyy, 69% of immunity and a triplex XXXxYYYY, 96.4% of immunity. Therefore, the superiority of multiplex progenitors is evident as they practically solve the problem of both PVX and PVY infections.

Inheritance of resistance to PLRV is complex and not as well known as that of PVX and PVY. Several mechanisms have been described as resistances to infection, multiplication, translocation, insect vectors, etc. The most studied resistance to infection would be polygenic and inherited with a sizable additive gene action reflected by its medium - high narrow sense heritability, \( h^2 = 0.69 \), that ensures an important response to selection (Salas, 2007).

**Breeding philosophy**

Potato production in most areas of the developing world is based on foreign cultivars often susceptible to virus diseases. Farmers of the countries where the seed originate avoid virus damage planting healthy seed. However, a primary cause of low potato productivity in most developing countries is the use of infected seed-tubers, due to high cost, scarcity or lack of certified seed. Since PLRV, PVY and PVX are major agents of “crop degeneration” reducing tuber yield and quality, selection of resistant varieties and assembly of superior progenitors for their breeding programs is the only economic solution (Mendoza, 1989a).

**Sequential breeding strategy**

To accomplish the objective of selecting high performing multiple virus resistant cultivars, a pragmatic strategy with modifications to traditional breeding methods was designed.

1. Testing and selecting a large number of clones under diverse environments to search for wide adaptation to day length and higher temperature,

2. Progeny testing clones selected in (1) for general combining ability (GCA) to identify those transmitting their traits to a high proportion of progenies (Mendoza, 1980)

3. Growing seedlings in the greenhouse under 16 hours of day length to improve adaptation to medium and long days followed by testing under warm environments,

4. Since the genetic control of PVX and PVY immunities was simple while that of PLRV was more complex, the work was split in two phases applied sequentially at different times:

   a. Start combining PVX + PVY immunities to breed multiplex selected progenitors and

   b. Crossing PVX+PVY immune with the PLRV resistant progenitors, selected by progeny testing, to develop high yielding multiple virus resistant varieties (Mendoza et al, 1989b).

**Genetic resources for the breeding work**

Immunities to PVX and PVY came from *S. tuberosum* L. ssp. andigena native cultivars (Huaman, 1980, Gálvez et al., 1992) and long day adapted *andigena* (*Neo tuberosum*) developed at USA (Plaisted, 1980). An additional input of *neo-tuberosum* was the late blight resistance and higher temperature adaptation besides virus resistance. Additional PVX immunity came from a few US and European cultivars derived from *S. acaule* and PVY immunity from a few clones bred in Europe derived from *S. stoloniferum* (Mendoza, 1989).
Resistance to PLRV infection had a wider genetic origin with an important contribution of wild species, particularly *S. demissum*. Commercial resistant varieties and breeding clones imported from Argentina, Chile, UK, Germany, Scotland, Netherlands, Poland, etc., were included.

**Breeding results**

*Stepwise assembly of multiplex PVY and PVX+PVY immune progenitors*

(i). *Why multiplex progenitors?* Crossing *triplex* (XXXxYYyY) to a susceptible (xxxxyyyy) clone produce 96.4% of immunity to both viruses. Therefore, using *triplex* progenitors avoids an expensive and time consuming screening as near all progenies are immune and provides a total genetic control of these viruses and facilitates combining with resistance to important diseases as leaf roll, late blight, etc. (Mendoza, 1993).

(ii). Initial crosses of (PVX imm.) x (PVY imm.) clones: (XXXXyyyy) x (xxxxYYYY) ⇒ ¼ XXXxYYYY : ¼ XXXyyyy : ¼ xxxxYYYY : ¼ xxxxyyyy. Seedlings were inoculated with a mix of both viruses. The *simplex* PVX + PVY immune did not show symptoms and were field evaluated and selected for agronomic traits and their immunity was verified by grafting and ELISA testing...

(iii). Crossing high yielding, early maturing, heat tolerant to *simplex* PVX + PVY progenitors: (xxxxyyyy) x (xxxxYYYY) ⇒ 1/4 Immune to both X and Y : 3/4 susceptible to either X or Y or both. Immune clones were tested for yield, tuber quality, and earliness, and the selected rechecked by grafting and then progeny tested to determine their parental value. The outcome was selecting outstanding progenitors: XY.4, XY.9, XY.13, XY.16, XY.20, LT-8, LT-9, 7XY.1, etc.

(iv). Crossing *simplex* (XXXxYYYY) x (XxxxYYYY) ⇒ 9/16 imm.: 7/16 susc. Of the 9/16 immune only 1/9 was *duplex* and identified back crossing to a susceptible tester. Field testing, rechecking for immunity and assessing parental value followed.

(v). The most complex phase was intercrossing *duplex* to select *triplex* and *quadruplex*. (XXxxYYYY) x (XxxxYYYY) ⇒ 1225/1296 imm.: 71/1296 susc. Out of the 1225/1296 immune it was expected only 6.25 *triplex* or *quadruplex*. The clones identified were *triplex* at both loci. Outcomes: Highly selected PVX + PVY *triplex*: TXY.2, TXY.3, TXY.4, TXY.8 and TXY.11 are now available for breeders use.

**Combining PVX + PVY immunities with PLRV resistance**

General Combining ability field testing conducted at CIP, for PLRV resistance of several clones and cultivars permitted identifying excellent progenitors transmitting resistance to a high proportion of their progenies: Serrana and Pentland Crown (Brandolini et al, 1992), the CIP progenitors product of the strategy discussed are: LR93.156, [(G7445 x YY.1) x Y84.004], LR93.160 (Mariella x XY.13), and full sibs C93.154 and C93.156 [(Monalisa x YY.5) x Y84.004] (Salas, 2007) and Sedafin, Pirola, Bzura and Mex-32 (Mendoza, 2008).

As outputs of this breeding strategy that developed *triplex* immune PVY and PVX + PVY immune progenitors were crossed to previously identified PLRV resistant parents, several new varieties were released in Peru and other countries.

Virus resistant cultivars released in other countries: **IPORÁ** (Serrana x 7XY.1) in Uruguay, **CHAMAK** (Serrana x LT-7) in Bangladesh, **IRA-92** (Renska x 7XY.1) in Cameroon, **KINIGI** (65.ZA.5 x YY.1) in Rwanda, **MURUTA** (CFK-69.1 x 14XY.4) in Burundi, etc.
Table 1. High yielding, early maturing and virus resistant varieties released in Peru in the last 15 years

<table>
<thead>
<tr>
<th>Variety</th>
<th>Female</th>
<th>Male</th>
</tr>
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<tbody>
<tr>
<td>Costanera</td>
<td>LT-1 (Katahdin x Aquila)</td>
<td>(PVY + PVX Bulk)</td>
</tr>
<tr>
<td>Tacna</td>
<td>Serrana (Argentina)</td>
<td>XY.4</td>
</tr>
<tr>
<td>Maria Bonita</td>
<td>378015.18</td>
<td>PVY Bulk</td>
</tr>
<tr>
<td>Basadre</td>
<td>Sedafin (Chile)</td>
<td>388809.2 (Y84.007 x Y84.020)</td>
</tr>
<tr>
<td>Primavera</td>
<td>B-71-74-49.12 (Argentina)</td>
<td>385280.1 (LT-8 x 575049)</td>
</tr>
<tr>
<td>Única</td>
<td>387521.3 (AVRDC-1287.19 x 7XY.1)</td>
<td>Aphrodite (Netherlands)</td>
</tr>
<tr>
<td>Reiche</td>
<td>MEX-32 (Mexico)</td>
<td>XY.9</td>
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An important outcome of the strategy is the variety TACNA selected for earliness, yield, agronomic characters and PVX and PVY immunities and PLRV resistance in San Ramón and La Molina and later in Tacna, a southern semi arid testing site in Peru, where it showed moderate tolerance to salinity and drought. It was renamed as COOPERATION-88 in China and planted in 120,000 ha in 2007 becoming the largest adopted CIP-breed variety worldwide (CIP Newsletter, 2009). Recognition should be given to the late Dr. Rene Chavez (University of Tacna) who collaborated with the author in its evaluation. Tacna’s progenitors are (Serrana x XY.4). XY.4 is an important progenitor developed in CIP with parents: LT-8 [LT-1(Aquila x Katahdin) x PVX+PVY Bk.] x TS-4 [377887.17(N567.8 x R-704.19) x LT-7]. Progenitors LT-1, LT-7, LT-8 and TS-4 were bred in Peru within this strategy.

Additionally, CIP has bred several clones immune to PVX and PVY and resistant to other diseases derived from the triplex, i.e., TXY.8 x 387170.9 (bacterial wilt), TXY.3 x India-1039, (highly resistant to late blight), TXY.2 x 104.12LB (bacterial wilt), etc.

At present, within a special project, a population developed crossing triplex TXY.3, TXY.6 and TXY.11 to late blight resistant progenitors is under field evaluation. Selection is being carried out for agronomic and tuber traits and blight resistance with no need to screen for PVX and PVY as the great majority of clones should be immune to both viruses.

Conclusions

(1). Development of a breeding philosophy and a pragmatic breeding strategy using some arguments different to those of traditional potato breeding to select varieties for the developing world. Early maturity, tuber yield and quality, adaptation to stressing environments and disease resistances were mayor objectives pursued.

(2). Developing highly selected simplex, duplex and triplex PVY and PVX+PVY immune progenitors. The last group transmits their joint immunity to 96.4% of progenies when crossed to any susceptible genotypes, simplifying breeding for multiple resistances to important diseases.

(3). From advanced clones developed at CIP as a result of (1) and (2), release by national programs in Peru and other countries several new commercial varieties of early maturity, high yield and tuber quality, PVX+PVY immunity and some also resistant to PLRV.

(4). It is hoped that CIP continues selecting new triplex progenitors and enhances their use to select the highly needed multiple resistant varieties for the developing countries, such as the long time due Late blight+PLRV+PVY+PVX.
Literature cited


