

Varying Levels of Susceptibility to Late Blight in Ecuador

- Relation between Resistance and the Need for Fungicide Application

Jenny Knutsson



Varying Levels of Susceptibility to Late Blight in Ecuador- Relation between Resistance and the Need for Fungicide Application

Jenny Knutsson

Supervisor: Jonathan Yuen, Department of Forest Mycology and Plant Pathology, SLU

Assistant Supervisor: Arturo Taipe, Centro Internacional de la Papa, Quito

Examiner: Dan Funck Jensen, Department of Forest Mycology and Plant Pathology, SLU

Credits: 15 hec

Level: Basic

Course title: Independent project/degree project in Biology

Course code: EX0418

Programme/education: Agriculture Programme – Soil and Plant Sciences

Place of publication: Uppsala

Year of publication: 2011

Picture Cover: Potato plant in the Andes, photo by Jenny Knutsson

Online publication: <http://stud.epsilon.slu.se>

Key Words: Phytophthora infestans, potato, computer simulation, simulation model



Swedish University of Agricultural Sciences
Faculty of Natural Resources and Agricultural Sciences
Department of Forest Mycology and Plant Pathology

Abstract

Potato late blight is a devastating disease in potato production all over the world and constitutes the major biological yield limiting factor in Ecuador. The disease is generally controlled chemically and a large proportion of the total potato production cost in Ecuador is due to fungicides. Potato late blight is also controlled by disease escape. A third alternative when it comes to protecting the crop from late blight is to cultivate varieties resistant to the disease. However, most Ecuadorian farmers still use varieties with a high susceptibility to late blight. Furthermore even resistant varieties are frequently treated with large amounts of fungicides, often due to lack of knowledge about the adequate amount needed. Successful disease management is a very important factor in order to increase productivity and reduce production costs for resource-poor farmers, and one part of this is to quantify the amount of fungicide application needed for different varieties of potato.

In this experiment field trials with 12 varieties of potato were performed in Quito, Ecuador. A recently developed scale was used to evaluate the level of susceptibility to potato late blight among the different varieties. The results provided new information about some of the potato cultivars and may lead to an increased cultivation of varieties with a higher level of resistance to the disease. The effect of resistance when it comes to the need of fungicide application was also evaluated. The trial showed that varieties with a high resistance to the disease had a reduced demand for chemical treatment. Finally, a computer simulation model, LATEBLIGHT, was validated for Ecuador. Computer simulations were compared to epidemics observed in the field trial and the level of agreement was generally high. Usage of the model is likely to save a lot of time and money in future crop breeding programs and evaluations of different management practices.

Table of contents

Abstract	3
Table of contents	5
1 Introduction	7
1.1 Background	7
1.2 Potato Late Blight	8
1.2.1 <i>Phytophthora infestans</i>	10
1.2.2 Symptoms of Potato Late Blight and Tuber Blight	12
1.2.3 Resistance to Potato Late Blight	13
1 Objective	16
2 Materials and methods	17
2.1 Quantification of resistance to <i>Phytophthora infestans</i>	18
2.2 Relation between resistance and need for fungicide application	20
2.3 Validation of computer simulation	21
3 Results	22
3.1 Quantification of resistance to <i>Phytophthora infestans</i>	22
3.1.1 Conclusions.....	24
3.2 Relation between resistance and need for fungicide application	24
3.2.1 Varieties with susceptibility level 4	24
3.2.2 Varieties with susceptibility level 5	27
3.2.3 Varieties with susceptibility level 6	30
3.2.4 Varieties with susceptibility level 7	34
3.2.5 Varieties with susceptibility level 8	38
3.2.6 Conclusions.....	41
3.3 Validation of computer simulation	41
3.3.1 Conclusions.....	47
4 Discussion	48
4.1 Quantification of resistance to <i>Phytophthora infestans</i>	48
4.2 Relation between resistance and need for fungicide application	49
4.3 Validation of computer simulation	50
References	51
Acknowledgement	54

1 Introduction

1.1 Background

Cultivation and consumption of potato has increased in the developing countries during the latest decades, and potato constitutes the fastest growing of the major food crops worldwide (International Potato Center, 2006). After rice, wheat and maize, potato ranks fourth among global food crops in terms of production (FAO, 2008).

The potato originates from the Andes of South America and is perennial in its native habitat. Due to an intensive breeding it can nowadays be cultivated in most parts of the world, although it is still best adapted to the cool temperate regions of the high altitudes (2000-3500 masl) in the Andes, and at sea level in the temperate zones of North America, Europe, southern Chile and Argentina. There is a great genetic richness in wild species, which are found in a much wider range of habitats, and over wider latitude than cultivated species. Some of them endure and survive in very extreme conditions, from dry deserts where they have to withstand considerable drought and heat, to altitudes of 3500-4500 masl in the high Andes where they exhibit strong frost tolerance. Wild potatoes also show a greater range of adaptation to pests and pathogens, and these qualities are of great interest to plant breeders in order to develop more sustainable varieties of cultivated potatoes (Harris, 1992).

Potatoes are an essential dietary staple for many Andean people. About 200 different varieties of potato exist in Ecuador, although just a fraction of them are cultivated commercially (Taipe, pers.com., 2010). In order to meet the demands of the growing urban population in Ecuador potato production has become more commercially specialized. However, potato remains a crop for small scale farmers

(Mancero, 2007). The soils and climate provide favourable yield conditions, and in theory there could be harvests of up to 60 tonnes/ha, but in reality official yield estimates about 10 tonnes/ha (Taïpe, pers. com. 2010). The low yields are due to many biotic, abiotic and social constraints, but the main biologically yield limiting factor is considered to be potato late blight (Forbes et al, 1997).

The International Potato Center (CIP) is an international organization that aims to reduce poverty and hunger, and seeks to achieve sustainable food security in developing countries. One of the most important goals of CIP is to decrease the usage of harmful pesticides, particularly in potato production. CIP researchers strive to breed new disease-resistant potato varieties, suitable to the local conditions. In order to cope with late blight in an effective way it is also important to increase the local farmers knowledge of the disease, and of how best to complement the resistant cultivars through management techniques (International Potato Center, 2010). CIP scientists develop strategies, methods, and training materials for participatory research and farmer training. Simple decision-support systems are also developed and tested at CIP. These systems aim to help farmers make improved decisions about fungicide treatment and other management techniques (Forbes, pers.com., 2009). Successful disease management is considered to be a very important factor for poor farmers in order to increase productivity, reduce production costs, and mitigate negative impacts on health and environment (Nelson et al, 2001).

1.2 Potato Late Blight

Potato late blight is a disease that affects the entire potato plant. It is caused by the pathogen *Phytophthora infestans* that after infection produces a mycelium inside the leaves from where it can then be spread (Andersson and Sandström, 2000). Infection in leaves and stems reduces the plants ability to photosynthesise, and thereby the yield potential. Late blight first occurred in Europe in the mid 1840s. Ever since then there have been numerous studies throughout the world of the etiology, epidemiology and means of control of the pathogen causing the disease. The intensity of the research increased as a new mating type of the pathogen arrived to Europe in 1984 (Pérez and Forbes, 2008).

The disease is generally controlled by usage of protective fungicides that have no curative ability. The intervals between sprayings are therefore usually short, 5-7 days, and this leads to a great impact on the environment and on the economy of the farmers (Govers et al., 2009). It is estimated that Andean farmers spend 5-20%

of their total production costs on late blight fungicides (Kromann et al, 2009). The most commonly used chemical in Ecuador is the broad spectrum fungicide Mancozeb (Cole et al 2002), which is approved by the United States Environmental Protection Agency. However, it is highly recommended to use personal protection equipment while handling the chemical (EPA, 2005). Maneb and Chorothanlonil are other frequently used fungicides and together with Mancozeb they are considered dangerous to the health of the farmers, especially when not handled properly (Wesseling et al., 2005). According to Cole et al. (2002) Ecuadorian farmers often neglect the importance of personal protection. Pesticides are generally applied using backpack sprayers and gloves and protection clothing is not used very frequently.

Many small-scale peasant farmers in the tropical highlands lack financial resources, and a large part of the potato production is not treated against late blight chemically. These farmers usually control late blight by disease escape, i.e. growing the crop partly outside of the rainy season when the environment is less favourable for the disease. However, these conditions are also less favourable for potato cultivation, and disease escape practice may result in major yield losses; sometimes the crop is totally destroyed (Andrade-Piedra et al., 2005a). Large amounts of the potato production in Ecuador occur at altitudes ranging from 2400-3800 masl. At higher altitudes, above 3600 masl, there is a reduced risk for potato late blight, mainly because of lower temperatures that restricts the growth of the pathogen. Due to this an increasing proportion of the potato cultivation is taking place in these higher altitudes (Oyarzun et al., 2001; Andrade-Piedra et al., 2005a). This area is called *paramo*, and constitutes high-altitude grassland with tundra vegetation. The ecosystem is highly sensitive and contains large parts of the nation's water resources. In order to protect these sensitive ecosystems increased cultivation in the area is not desirable. Furthermore it is not an optimal area for potato production, reduced risk for late blight set aside, since the low temperatures imply an increased risk for frost. Because of the cold climate the potato crop also requires more time to mature at these heights (Taipe, pers.com., 2010).

Late blight can also be controlled by usage of resistant potato varieties. Experiments have shown that it is possible to reduce the usage of fungicides in late blight control by exploiting the host resistance (Naerstad and Hermansen, 2010). However, most Ecuadorian farmers still cultivate varieties susceptible to late blight and resistance levels of the most commonly used varieties are rarely sufficient (Andrade-Piedra et al., 2005a, Kromann et al., 2009). Furthermore even the resistant varieties are often treated with large amounts of fungicides, due to lack of

knowledge about the adequate amount needed (Cole et al., 2002; Taïpe, pers.com., 2010).

1.2.1 *Phytophthora infestans*

Potato late blight is caused by the pathogen *Phytophthora infestans*, which is an oomycete, unrelated to true fungi. The reproduction of the pathogen is usually asexual, but when compatible strains of opposite mating types are present sexual mating can occur (Andersson and Sandström, 2000). The pathogen is spread by wind and water-splashes, or by infected potato tubers. It infects and colonizes the host plant rapidly and effectively, and can destroy all above ground parts of a potato crop in less than a week and lead to severe quantitative yield losses (Andersson et al., 2009).

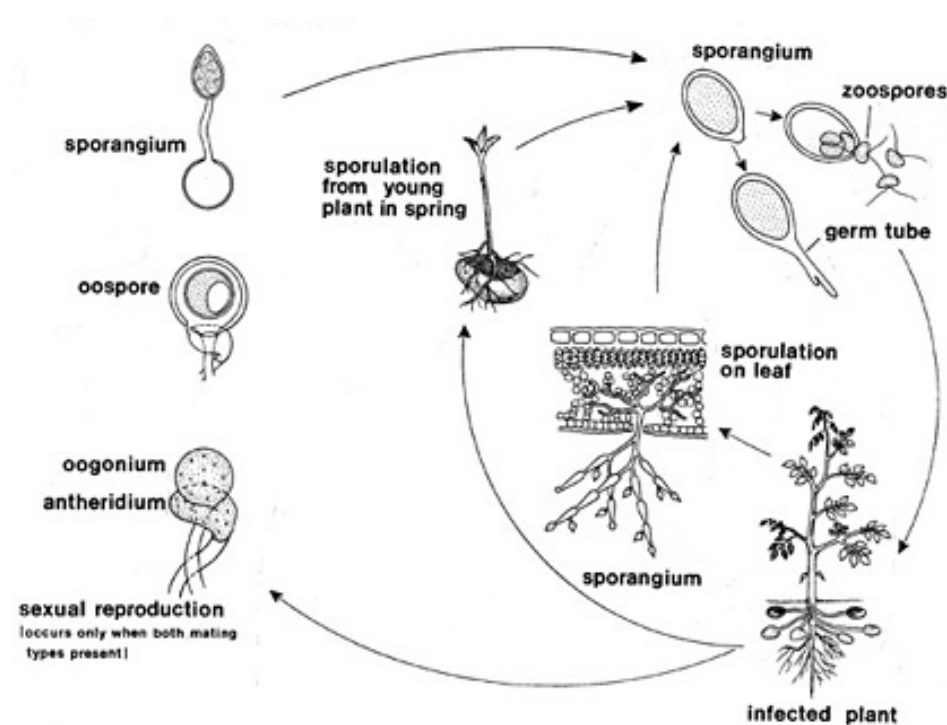


Figure 1. Life cycle of *Phytophthora infestans* (American Phytopathological Society, 2011).

Asexual reproduction

The asexual reproduction of *P. infestans* is rapid and is sometimes completed in only 4 days (Pérez and Forbes, 2008). Hence, there might be several asexual generations of *P. infestans* during one single growing season. Under favourable condi-

tions, i.e. temperatures between 10-25°C and a relative humidity of 100% or leaf wetness, the oomycete sporulates and produces spores able to infect potato foliage and potato tubers (Figure 1).

Sporangiophores are formed on the mycelium and grow out of the stomata openings of the leaves, and on them lemon shaped sporangia are borne. The sporangia can dislodge from the sporangiophores and be spread to nearby plants with wind or through water-splash. Sporangia are sensitive to solar radiation, but if protected from this they can survive for hours even in unfavourable conditions and can therefore be dispersed long distances; hundreds of meters or even kilometres (Andersson and Widmark, 2008). However, sporangia cannot survive in soil for long (Andersson and Sandström, 2000).

The sporangium germinates new plants either directly or indirectly. At temperatures above 20°C the germination is direct. The sporangium enters the plant cell either by forming an apressorium that penetrates the cell wall, or via stomata. At lower temperatures an indirect germination occurs. Each sporangium then releases 8 to 12 zoospores, which are able to move in water films with the help of flagella (Pérez and Forbes, 2008, Andersson and Sandström, 2000). Under favourable conditions zoospores can swim for hours before they germinate plant cells. After the infection a mycelium is formed. The mycelium grows within the cells and *P. infestans* establishes a parasitic relationship with the plant that lasts several days (Henfling, 1987).

Sexual reproduction

Sexual mating results in persistent oospores, which have an increased capacity of survival, and thereby also an increased capacity of transmitting the disease to surrounding potato plants (Andersson et al., 2009). Production of oospores enables late blight to spread not only by plantation of infected tubers, or by wind or water-splash-borne sporangia, but also by infested soil (Andersson and Widmark, 2008). Sexual reproduction also increases the genetic variation of *P. infestans*. This could possibly lead to a late blight of potato that is more aggressive in the field due to a faster spread and faster development of symptoms, and less sensitive to chemical substances (Andersson and Widmark, 2008; Andersson et al., 2009).

Tuber Blight

Under very wet conditions, i.e. heavy rains or irrigation, sporangia and zoospores can be rinsed off the haulm down into the soil where they infect the potato tubers. This causes tuber blight. The tubers might also be infected during harvest,

if they are exposed to infected haulm, or to sporangia present in the soil (Pérez and Forbes, 2008). The infected tubers host the oomycete until they sprout. The infected tubers give rise to new epidemics the following season. Potato tubers are important in the survival of the asexual phase of *P. infestans*, and for its overwintering in cold temperate zones. They also enable *P. infestans* to disperse long distances, as they are transported in vehicles and overseas. However, the general frequency of tuber infection is low in Ecuador, and tubers do not appear to be an important source of inoculums in the country (Oyarzún et al, 2005).

1.2.2 Symptoms of Potato Late Blight and Tuber Blight

Lesions become visible a few days after infection of the potato plant. The exact time depends on the genetic composition of the host and pathogen in combination with temperature.

Leaves

The first lesions on the leaves are small and green. As the mycelia grow between the cells dark brown watery looking spots appear on the leaves and stems (Figure 2). The lesions consist of necrotic tissue and on the leaves they are often surrounded by a yellowish green chlorosis (Cáceres et al., 2008). The necrotic lesions will continue to grow and will eventually blight the entire leaf.



Figure 2. Late blight on potato; leaves and stem infected. (Photo: Jenny Knutsson)

Under humid conditions, the lesions are also surrounded by a whitish mildew. This is the sporangiophores growing out of the leaf tissue (Henfling, 1987). Infected plants have a characteristic odour caused by the rapid decomposition of the plant tissue (Pérez and Forbes, 2008).

Stems

Infected stems show dark brown necrotic lesions, 5-10 cm long, generally in the upper third of the plant. The leaves may wilt above the point of the lesion. Infected stems become brittle and may break at the lesion point. Under humid conditions

sporulation might occur. The lesions are then surrounded by whitish mildew, but the mould is not as deep as in infected leaf tissue (Pérez and Forbes, 2008).

Tubers

As the infection reaches the tubers they get an irregular change in colour on the surface. Necrotic, brown lesions penetrate the tubers from the outside and in. As the infection proceeds the tuber might get infected with fungi and bacteria, which obstructs diagnostics (Pérez and Forbes, 2008).

1.2.3 Resistance to Potato Late Blight

There are two different types of resistance to potato late blight. Specific (vertical) resistance is effective against certain races of *P. infestans* and reduces the initial inoculum of the pathogen (Umareus and Umareus, 1994; Wastie, 1991). However, *P. infestans* is a plastic pathogen that easily forms new races. When a potato variety with vertical resistance is commonly grown the pathogen can adapt and form an abundance of races that are able to attack the variety in question. Due to this natural selection the advantages of vertical resistance often wears off with time (Van der Plank, 1963).

General (horizontal) resistance on the other hand is effective towards several races of *P. infestans* (Umareus and Umareus, 1994; Wastie, 1991). It operates by reducing the infection rate of the pathogen. A potato plant with horizontal resistance is more resistant to spore establishment, lesions formed by spores of *P. infestans* grow more slowly and the pathogen produces fewer sporangia. When the two types of resistance are combined the effects of specific resistance are enhanced by the general resistance. The general resistance also has a large impact on the effectiveness of fungicide application (Van der Plank, 1963). Current breeding strategies focus on general resistance in order to produce varieties that can be used in a sustainable potato production (Kamoun et al., 1998).

Evaluation of susceptibility to Potato Late Blight

In the highland tropics resistance classification is often problematic. European reference cultivars cannot be used, since they are poorly adapted to short day lengths. Some breeders at the CIP have selected domestic cultivars that are used to improve estimation of resistance, but the process is not standardized throughout the organization, and much less among other potato breeding programs (Yuen and Forbes, 2009).

Resistance is indicated by the susceptibility to late blight of a plant. The area under the disease progress curve (AUDPC); or the percent leaf area affected by disease, is a quantitative summary of disease intensity over time and can be used for estimation of susceptibility. Yuen and Forbes (2009) have developed a scale to evaluate resistance to disease in plants, with ascending values corresponding to increasing susceptibility to late blight. Thus, no disease development represents the highest level of resistance. The evaluation of susceptibility in this 1-to-9 scale is based on AUDPC and is adapted to the environmental conditions in the highland tropics. Since AUDPC combines information about several aspects of the epidemic, i.e. inoculum, environment and host susceptibility, some alteration needs to be done in order to evaluate susceptibility alone. Relative AUDPC (RAUDPC) is one way of modification which provides a more stable measure of cultivar performance (Yuen and Forbes, 2009).

Computer simulation with LATEBLIGHT

Development of control strategies for specific locations, seasons, potato cultivars and pathogen populations is difficult and requires extensive field experimentation. Computer-based simulation models may be an effective way to reduce costs and labour intensity (Andrade-Piedra et al., 2005a). Computer simulations provide an increased understanding of disease epidemiology in diverse environments, and enable rapid evaluation of disease management strategies (International Potato Center, 2010). LATEBLIGHT is a mathematical model created at Cornell University in the early 1980s, and it is one of the most extensively used simulation models. The model was originally written in FORTRAN (Bruhn and Fry, 1981), but several versions have been developed since then. In the latter years it has been modified to suite the conditions in the tropical highlands. In order to validate the model for this area simulated data needs to be compared with observed data (Andrade-Piedra et al., 2005a; Andrade-Piedra, 2006).

The LATEBLIGHT model can either be used in Statistical Analysis System (SAS) or POLUX. POLUX is a free-access version of LATEBLIGHT, created by CIP to increase the usability of LATEBLIGHT in less-developed countries where SAS is generally inaccessible. Weather variables are calculated by POLUX from data of rainfall, temperature and relative humidity that are measured with sensors. Date of the end of the epidemic, host-pathogen interaction, fungicide applications and initial inoculums (natural or artificial) are also taken into consideration in the model. POLUX is also able to import observed blight severity to compare with simulated blight severity (Andrade-Piedra, 2006).

1 Objective

This project had three general objectives. The first was to evaluate the level of resistance to potato late blight in twelve different potato varieties cultivated in Ecuador according to the susceptibility scale elaborated by Yuen and Forbes (2009).

The second objective was to evaluate this resistance in terms of fungicide application needs. The purpose of this was to provide quantitative measures of resistance for each of the varieties, and to increase the knowledge about the resistance levels and enlarge the precision of the resistance in order to grow the varieties best fitted to the surrounding circumstances, with as little use of fungicides as possible.

The third objective was to evaluate the correctness of disease simulations performed by the computer simulation model LATEBLIGHT. LATEBLIGHT has been adapted and qualified for use in the tropical highlands (Andrade-Piedra et al. 2005a, 2005b), but it needs to be tested more in this area in order to further evaluate the simulations.

2 Materials and methods

In order to achieve the objectives of the project a field trial was conducted. The trial was designed as a split-plot, with fungicide regime in the main plot and potato variety in the subplot, and contained three replications. The experimental units were formed as parcels with an area of 12 m². Four rows were planted in each unit with ten plants per row.

Twelve different varieties with reported differences in resistance towards *P. infestans* were used (Table 1). The sprouted tubers were planted 10 of February 2010. Each unit was surrounded by one meter of oats. Weed was controlled chemically 21 days after planting by application of Metribuzina (1l/200l) and Paracuat (0.2l/200l). The plants were hilled twice manually; 42 and 58 days after planting. The soil was fertilized according to recommendations from the Autonomous National Institute for Agriculture and Livestock Research in Ecuador (INIAP); 90 kg N, 300 kg P, 100 kg K and 50 kg S, Mg and other micro nutrients were also added. The potato plants were naturally infected with *P. infestans*. The experimental parcels were situated at CIP's experimental station in Quito, Ecuador, at an altitude of 3058 masl. Precipitation, temperature and relative humidity were registered by sensors placed in the field, 150 cm above canopy. Precipitation was large during the growing season of the field trial (Figure 3). This caused a high relative humidity (above 90%), and favorable conditions for establishment and development of late blight.

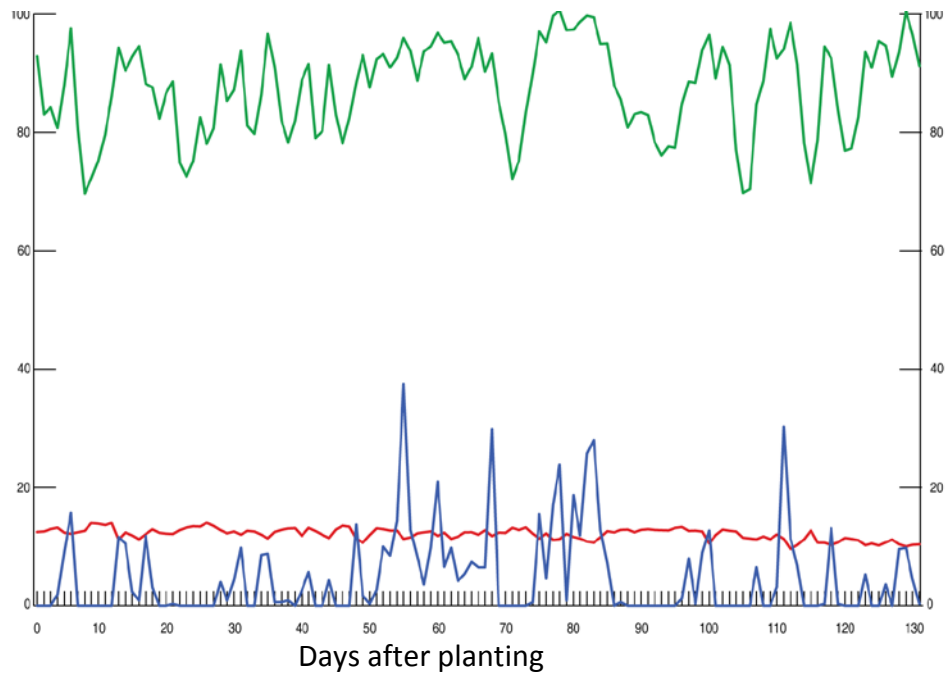


Figure 3. Daily measurements of climatic factors significant for the epidemic development of late blight. The green line shows the relative humidity (%), the blue line precipitation (mm) and the red line shows the average temperature ($^{\circ}\text{C}$) during the period.

Potato late blight was recorded at emergence, and the foliage severity was evaluated every seven days, as a percentage of the total foliage.

At the end of the trial the harvest was measured (kg/parcel). Total harvest (tonnes/ha) was calculated by use of number of plants harvested in each parcel, and measurement of biomass of three random plants in each parcel.

2.1 Quantification of resistance to *Phytophthora infestans*

Control parcels without fungicide application were used to evaluate the level of susceptibility of the different varieties according to the scale elaborated by Yuen and Forbes (2009).

Table 1. Evaluated potato varieties and their expected level of susceptibility to late blight

Variety	Level of susceptibility	Source	Country
Betina	moderately resistant	FEDEPAPA ¹	Colombia
Carolina	susceptible	CIP ²	Ecuador
Cecilia	moderately resistant	NA ³	Ecuador
I-Estela	susceptible	INIAP ⁴	Ecuador
I-Fripapa	moderately resistant	INIAP ⁴	Ecuador
I-Gabriela	very resistant	INIAP ⁴	Ecuador
Roja Nariño	susceptible	FEDEPAPA ¹	Colombia
I-Natividad	susceptible	INIAP ⁴	Ecuador
Nova	moderately resistant	CONGELAGO-CIP ²	Colombia
Superchola	very resistant	Manuel Bastidas ⁵	Ecuador
Suprema Pastusa	susceptible	FEDEPAPA ¹	Colombia
Única	moderately resistant	NA ³	Colombia

¹ Federación Colombiana de Productores de Papa

² Centro Internacional de la Papa (International Potato Center)

³ No source found

⁴ Instituto Nacional Autónomo de Investigaciones Agropecuarias del Ecuador (Autonomous National Institute for Agriculture and Livestock Research in Ecuador)

⁵ Private Investor

Based on AUDPC (percentage affected leaf area) the different varieties were given values from 1 to 9; ascending values corresponding to increasing susceptibility to late blight. The genotype that exhibited largest susceptibility in the field experiment served as a reference. The levels for the other varieties were calculated according to the formula:

$$\text{Scale value Gn} = (\text{RAUDPC Gn} / \text{RAUDPC Gs}) * 8$$

RAUDPC= relative AUDPC (percentage affected leaf area)

Gn= potato genotype

Gs= genotype with largest susceptibility

8= value of Gs

An analysis of variance was conducted with the RAUDPC values, and mean separation was examined by calculating the honest significant difference (HSD or Tukey test) (Quinn and Keough, 2002).

2.2 Relation between resistance and need for fungicide application

Five different intervals of fungicide application were evaluated. The contact fungicide Chlorothalonil (Balear 720) was used in various regimes according to Table 2 (2, 5 c.c active ingredient per litre water). The twelve potato varieties of varying susceptibility levels (Table 3) were treated with the different fungicide application intervals. The combination of factors resulted in 72 different treatments (Figure 3).

Table 2. Application intervals and number of applications

Intervals of application	Number of applications	Code
Control	0	I0
Every 4 days	25	I4
Every 8 days	13	I8
Every 12 days	8	I12
Every 16 days	6	I16
Every 20 days	5	I20

Table 3. Potato varieties evaluated

Variety	Level of susceptibility		Code
	<i>Prior estimation</i>	<i>Evaluation according to scale</i>	
Pastusa Suprema	susceptible	4	V1
I-Estela	susceptible	4	V2
I-Natividad	susceptible	5	V3
Nova	moderately resistant	5	V4
I-Fripapa	moderately resistant	6	V5
Carolina	susceptible	6	V6
Única	moderately resistant	6	V7
Betina	moderately resistant	6	V8
Roja Nariño	susceptible	7	V9
Superchola	very resistant	7	V10
I-Gabriela	very resistant	8	V11
Cecilia	moderately resistant	8	V12

1= V1xI0	19= V4xI0	37= V7xI0	55= V10xI0
2= V1xI4	20= V4xI4	38= V7xI4	56= V10xI4
3= V1xI8	21= V4xI8	39= V7xI8	57= V10xI8
4= V1xI12	22= V4xI12	40= V7xI12	58= V10xI12
5= V1xI16	23= V4xI16	41= V7xI16	59= V10xI16
6= V1xI20	24= V4xI20	42= V7xI20	60= V10xI20
7= V2xI0	25= V5xI0	43= V8xI0	61= V11xI0
8= V2xI4	26= V5xI4	44= V8xI4	62= V11xI4
9= V2xI8	27= V5xI8	45= V8xI8	63= V11xI8
10= V2xI12	28= V5xI12	46= V8xI12	64= V11xI12
11= V2xI16	29= V5xI16	47= V8xI16	65= V11xI16
12= V2xI20	30= V5xI20	48= V8xI20	66= V11xI20
13= V3xI0	31= V6xI0	49= V9xI0	67= V12xI0
14= V3xI4	32= V6xI4	50= V9xI4	68= V12xI4
15= V3xI8	33= V6xI8	51= V9xI8	69= V12xI8
16= V3xI12	34= V6xI12	52= V9xI12	70= V12xI12
17= V3xI16	35= V6xI16	53= V9xI16	71= V12xI16
18= V3xI20	36= V6xI20	54= V9xI20	72= V12xI20

Figure 4. Schedule of potato varieties, V, and fungicide application treatments, I. (See Table 2 and 3)

2.3 Validation of computer simulation

A version of the simulation model LB 2004 written in SAS (Andrade-Piedra et al., 2005a, 2005b) as well as another version implemented in Delphi and called POLUX (Forbes et al., 2008), was used to simulate disease development in the absence of fungicide application. These simulations were later compared with the observed epidemic development in the field trials without fungicide application.

3 Results

3.1 Quantification of resistance to *Phytophthora infestans*

By means of the weekly evaluations of percentage of foliage area affected by potato late blight relative AUDPC (RAUDPC) was calculated for each application interval in each potato variety (Table 4). Carolina, Nova and Única are early varieties and severity evaluations were possible 96 days after planting. Cecilia, I- Fri-papa and I-Gabriela are intermediate varieties and severity was evaluated 113 days after planting. Betina, I-Estela, Roja Nariño, Superchola and Pastusa Suprema are late varieties and severity evaluation was possible 126 days after planting.

Table 4. Evaluation of susceptibility to *P. infestans* in different varieties of potato

Variety	RAUDPC	Tukey value ¹	Level of susceptibility
Pastusa Suprema	0.34065	a	4
I-Estela	0.38367	a b	4
I-Natividad	0.41067	a b	5
Nova	0.45263	a b c	5
I-Fripapa	0.48886	b c	6
Carolina	0.48980	b c	6
Única	0.50190	b c	6
Betina	0.54966	c d	6
Roja Nariño	0.57062	c d e	7
Superchola	0.63476	d e f	7
I-Gabriela	0.69504	e f	8
Cecilia	0.72743	f	8

¹RAUDPC values followed by the same letter are not significantly different from each other based on Tukey's HSD.

Tukey values for the different measurements are shown in Table 4. Values followed by the same letters are not significantly different from each other when us-

ing Tukey's HSD. The Tukey test identified Pastusa Suprema as the variety most resistant to *P. infestans*, and Cecilia and I-Gabriela as the most susceptible varieties.

The epidemic development was low during the first 85 days in Pastusa Suprema (Figure 5). After this period there was a great increase and after another 40 days the affected foliage area reached 80%. The genotype I-Estela showed a similar behaviour. The conduct of I-Fripapa was also comparable, the difference was that the infection started to increase after 64 days, and the affected foliage area reached 100% within approximately 30 days. Cecilia and I-Gabriela both had low levels of infection during the first 45 days. Thereafter the infection grew rapidly and the affected foliage area reached 80% in just 20 days. The infection rate was stable for about one month, but 113 days after planting the affected foliage area reached 100%.

The evaluated genotypes formed five distinct groups, as shown in Table 4. Pastusa Suprema and I-Estela were least susceptible (level 4), I-Natividad and Nova were somewhat more susceptible (level 5), I-Fripapa, Carolina, Única and Betina showed larger susceptibility (level 6). Roja Nariño and Superchola (level 7), I-Gabriela and Cecilia (level 8) showed the greatest susceptibility to *P. infestans* observed in this experiment.

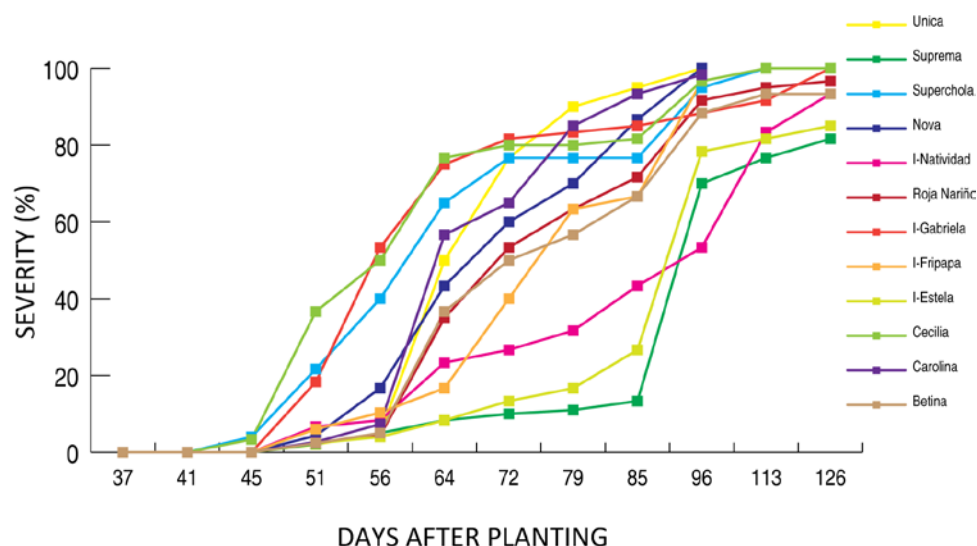


Figure 5. Epidemic development of late blight in 12 different varieties of potato. No fungicides applied.

3.1.1 Conclusions

The experiment showed that I-Gabriela and Cecilia were most susceptible to *P. infestans* (level 8). I-Fripapa, which is generally considered to be moderately resistant (Table 4), was valued as quite susceptible (level 7). Pastusa Suprema and I-Estela showed greatest resistance to *P. infestans* (level 4).

3.2 Relation between resistance and need for fungicide application

Different fungicide application intervals were used to evaluate the relationship between varying levels of resistance in the different potato varieties and the need for fungicide application. The different spray intervals gave varying results depending on the level of resistance in the potato variety. The optimum spray interval was defined as the one with the longest interval, but that still maintained effective disease control. For a specific fungicide treatment to be considered effective, the final disease level should not exceed approximately 20% at time of harvest. Furthermore a yield of approximately 20 tonnes/ha (about twice as high as the official yield in Ecuador) was required for a treatment to be considered effective.

3.2.1 Varieties with susceptibility level 4

Pastusa Suprema and I-Estela were the least susceptible varieties (Table 4). Both varieties were level 4 on the susceptibility scale (Yuen and Forbes, 2009). Different application strategies had similar effects on the two varieties (Figure 6). Only the intervals 4 days and 8 days (and 12 days in Pastusa Suprema) gave total protection against potato late blight. The intervals of 16 and 20 days provided protection during 96 days, but after this time the epidemic grew uncontrollably in these treatments.

The control treatment, without fungicide application, indicates that the registered disease level was very low during the first 50 days of the experiment. Thereafter a gradual increase of the epidemic occurred and lasted until day 85. This increase coincided with optimal conditions for establishment and development of potato late blight, and led to an extremely rapid growth of disease between day 85 and 96. During this period the affected foliage area reached 80%. The behavior of the disease was similar in treatments with fungicide application every 12, 16 and 20 days; although with fungicide application the disease development was less rapid.

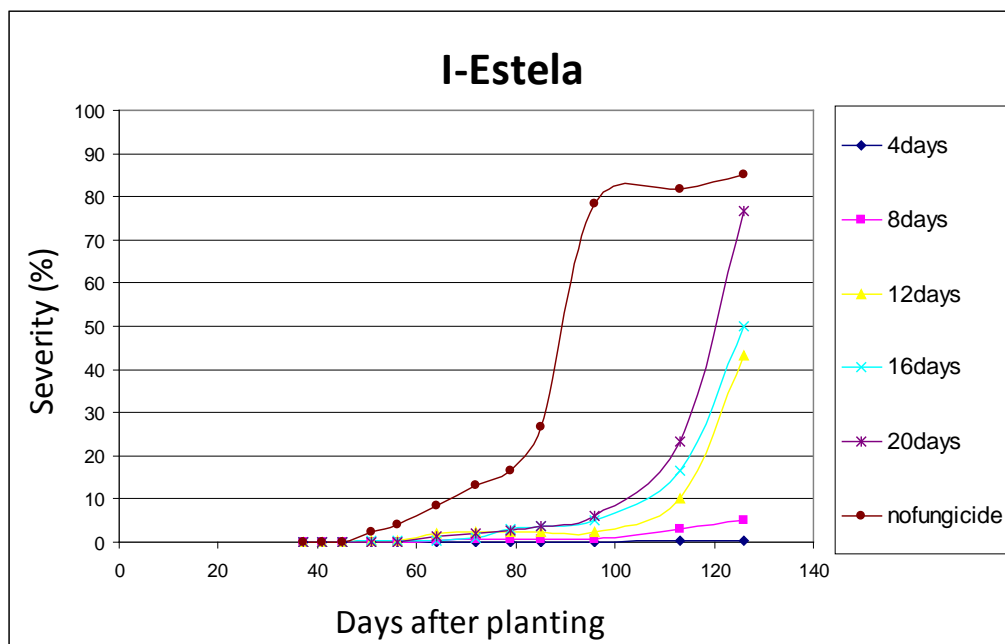
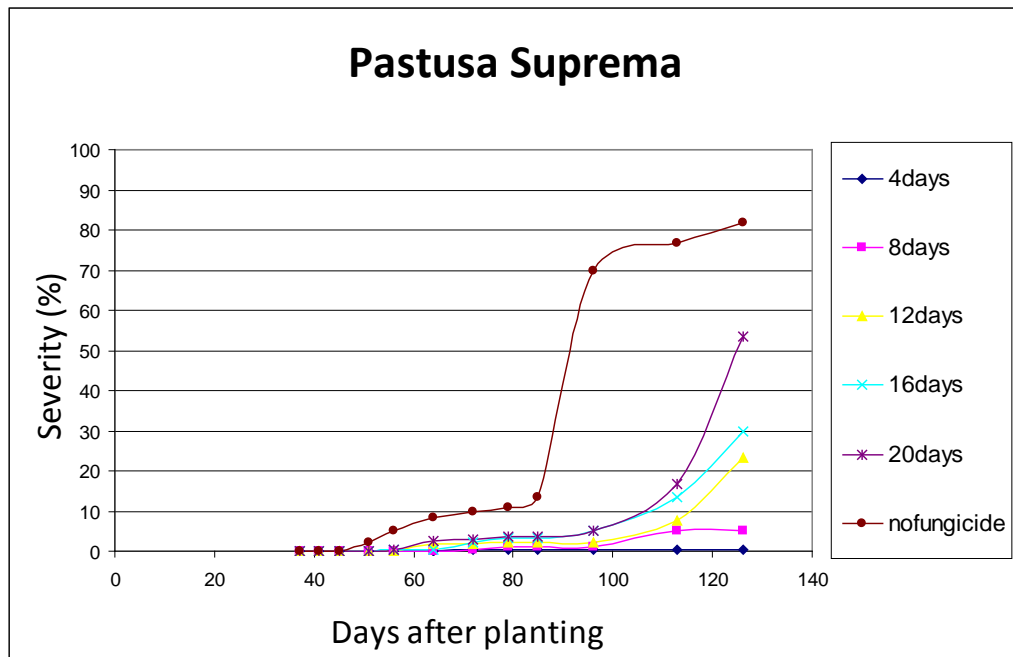


Figure 6. Development of late blight epidemic in varieties with susceptibility level 4 (Pastusa Suprema and Estela) with different intervals of fungicide application.

Pastusa Suprema was very resistant to the epidemic of late blight. Intensive protection (application interval of 4 days) led to yields of about 33 tonnes/ha, which

was four times as high as the yield of the parcels where no fungicides were applied (Figure 7). The no treatment parcels gave a yield of approximately 10 tonnes/ ha, which is equal to the mean harvest in Ecuador. With application intervals of 16 and 20 days the yield was reduced with about 10 tonnes/ha compared to application every 4 days. However, even with an application interval of 20 days the yields were twice as high as when no fungicides were applied.

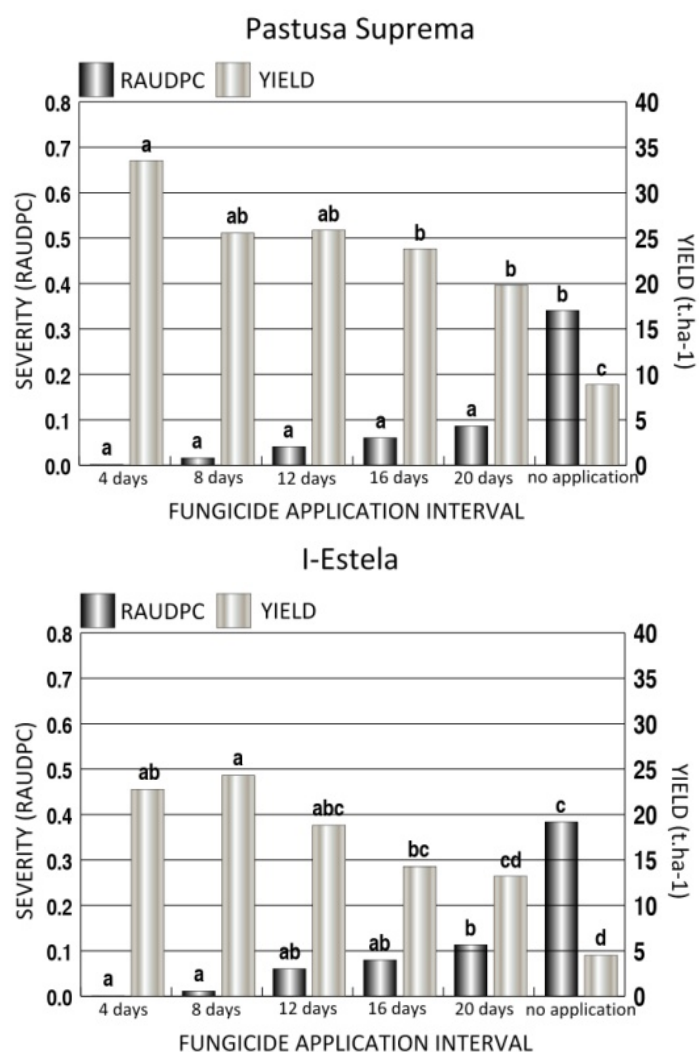


Figure 7. Averages and Tukey values (5%) for severity (RAUDPC) and yield (t.ha-1) for five different application intervals and control treatment in Pastusa Suprema and I-Estela (susceptibility level 4).

The yields of I-Estela were generally inferior to those of Pastusa Suprema. The yields of the application interval of 8 days were similar in both varieties, but an application interval of 4 days gave a much lower yield in I-Estela (Figure 7).

In varieties with susceptibility level 4 application intervals of 4 and 8 days provided almost total protection and yields of 25 to 33 tonnes/ha. However, these high application rates are not advisable due to their negative environmental impact and their high economic costs for the farmer. The most adequate application interval was between 12 and 16 days since these intervals provided a protection similar to treatments with shorter application intervals and the yields they rendered were up to three times as high as the yields from the treatment with no fungicide application.

3.2.2 Varieties with susceptibility level 5

According to the susceptibility scale, I-Natividad and Nova are rather resistant towards late blight (Table 4). The severity curves for the different treatments in I-Natividad show great similarity with the curves obtained for treatments in varieties with susceptibility level 4 (Figure 6). The difference is that in I-Natividad the epidemic in the control parcels started to increase after 56 days, i.e. 30 days earlier than in the varieties with susceptibility level 4 (Figure 8). The development for application intervals 12, 16 and 20 days were very closely related and in all cases the treatments stopped protecting the plants after 96 days. In Nova the disease started to grow without restraints 51 days after planting and after 96 days 100% of the foliage area was affected by late blight. Treatments every 4, 12, 16 and 20 days showed the same development. Fungicide application every 8 days protected the plants during 85 days, after this period the treatment lost effect.

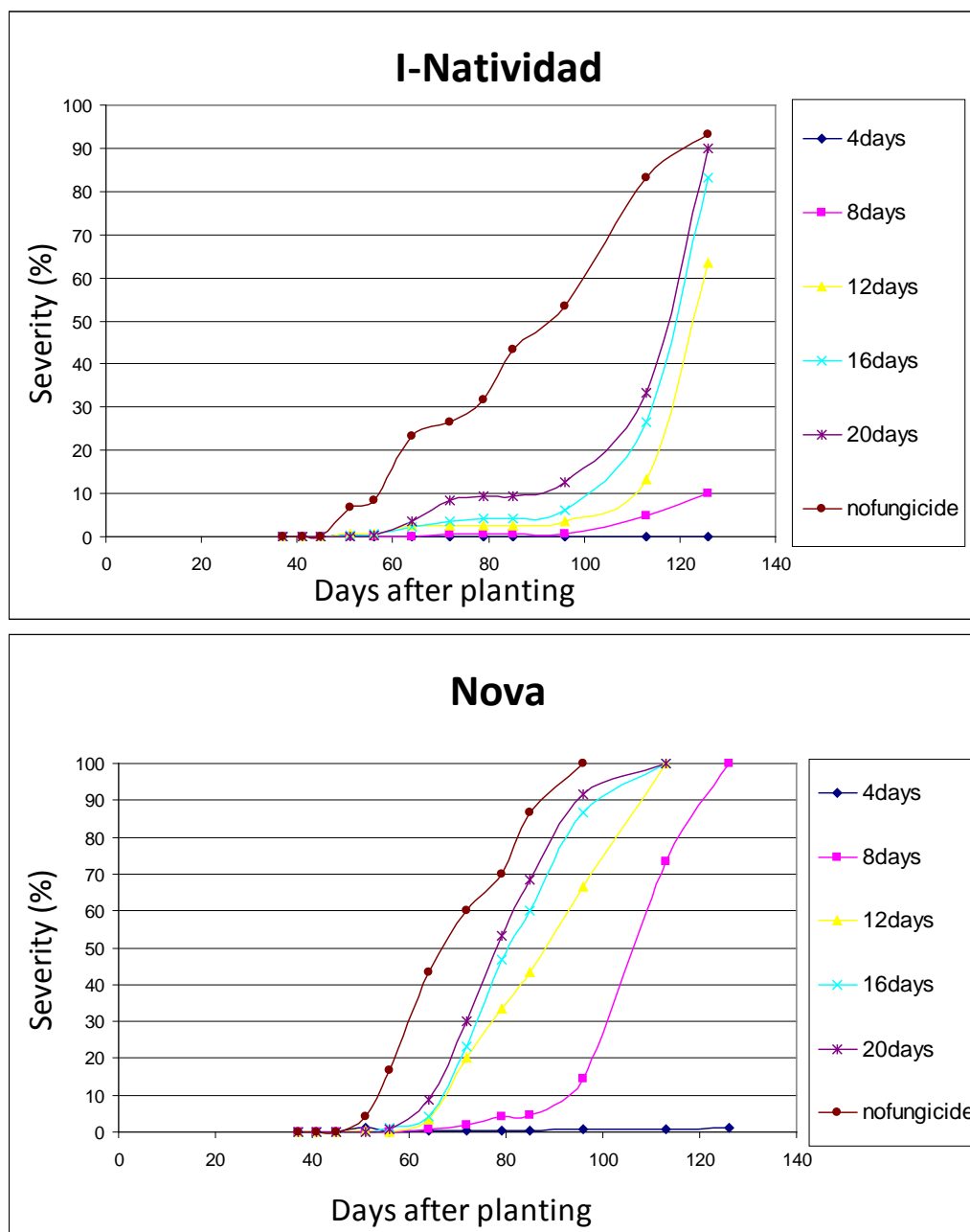


Figure 8. Development of late blight epidemic in varieties of susceptibility level 5 (I-Natividad and Nova) with different intervals of fungicide application.

Fungicide application intervals of 4 and 8 days provided improved protection and gave larger yields in I-Natividad (Figure 9). Application intervals of 12 days and more caused significant yield losses, up to 50%, due to increased late blight severity. Although fungicide application every 16 and 20 days generated higher

yields than application every 12 days the difference was not significant, and was probably due to some source of error in the 12 days treatment parcels. The parcels with application every 16 and 20 days generated yields of 17 tonnes/ha, which was three times as large as the control parcels without fungicide application. In Nova the yields decreased along with decreased protection in treatment every 4, 8, 12, 16 and 20 days. The yield from the parcels without fungicide application was very low, which indicates great susceptibility to late blight in this genotype and shows the necessity of maintaining the disease epidemic properly in order to gain sufficient yields.

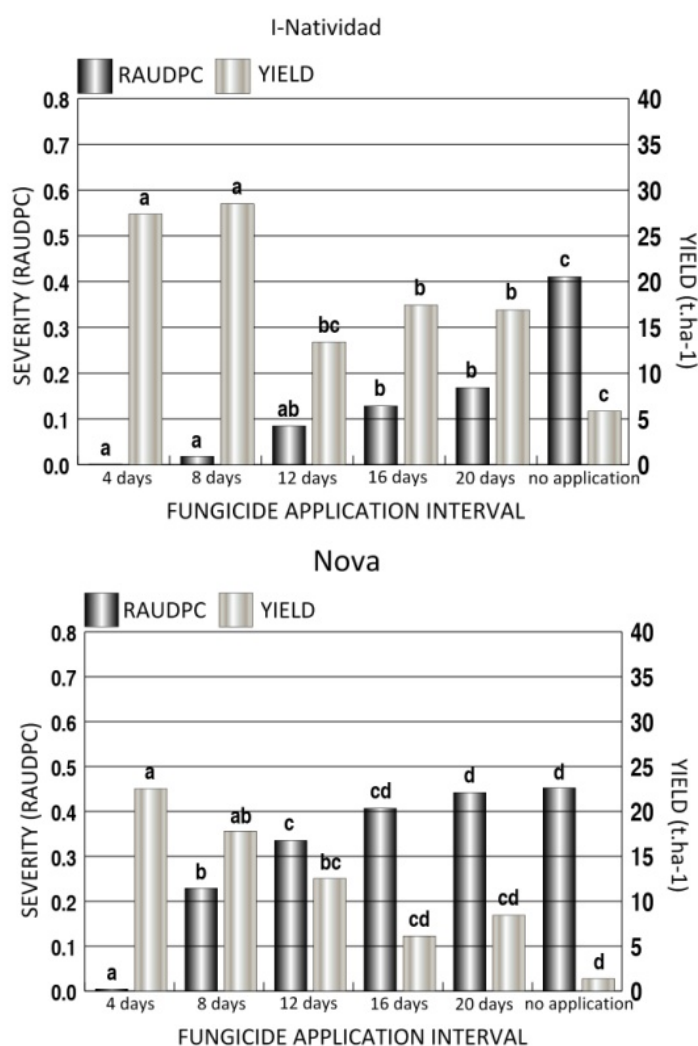
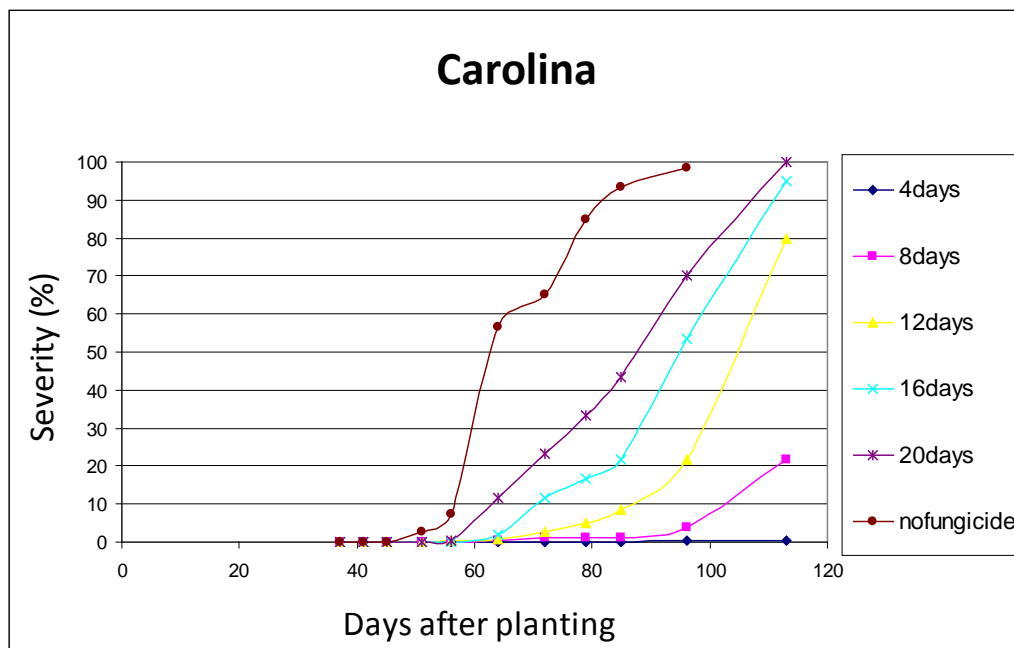
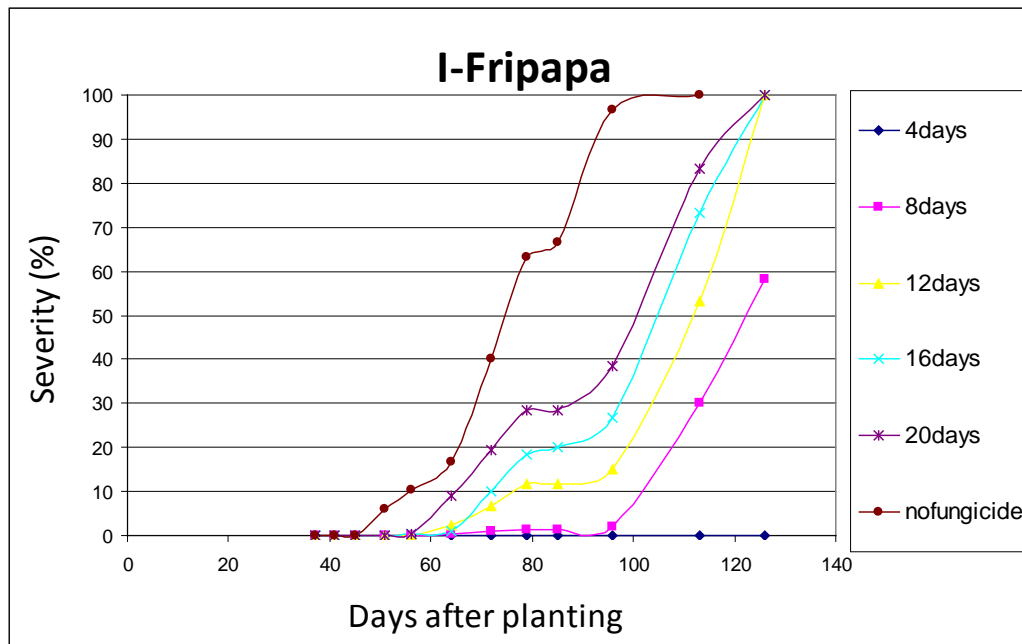


Figure 9. Averages and Tukey values (5%) for severity and yield (t/ha) for five different application intervals and control treatment in I-Natividad and Nova (susceptibility level 5).

In varieties with susceptibility level 5 treatments with fungicide application every 4 and 8 days were the only ones that gave satisfactory protection against late blight epidemics.

3.2.3 Varieties with susceptibility level 6

I-Fripapa, Carolina, Única and Betina all possesses level 6 on the susceptibility scale. In this group of varieties there was a great difference in protection between the different treatments. However, the different varieties behaved very similarly. Only an interval of 4 days provided satisfactory protection (Figure 10). An application interval of 8 days kept the disease under control during 85 or 96 days, but after this time the treatment was not sufficient.



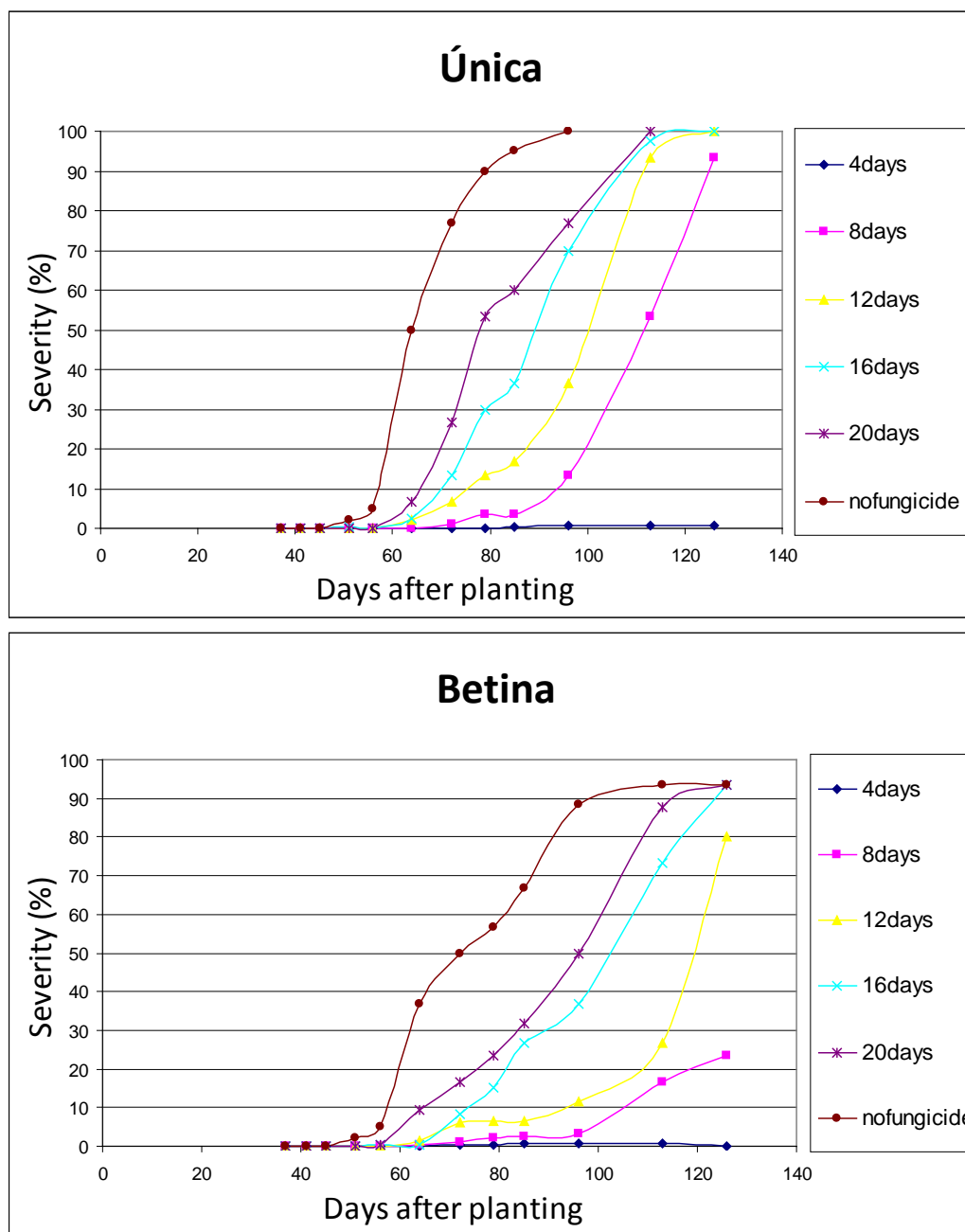
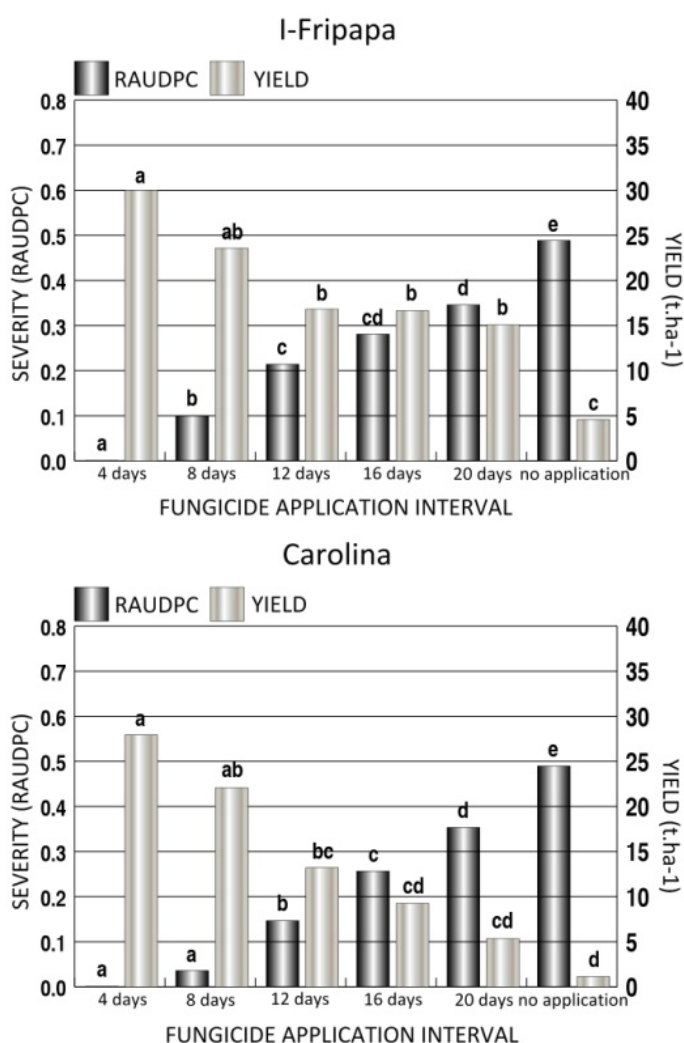


Figure 10. Development of late blight epidemic in varieties of susceptibility level 6 (I-Fripapa, Carolina, Única and Betina) with different intervals of fungicide application.

I-Fripapa and Carolina were similar in terms of severity and yields in each application interval (Figure 11). The protection given by fungicide application every 4 days generated highest yields. As the application interval increased to every 8

days the protection decreased and the yield was reduced by 21%. An application interval of 12 days gave a yield loss of 40-50% compared to an interval of 4 days. Application intervals of 16 and 20 days reduced the yield with 60 and 80% respectively. The registered severities in the varieties Betina, and above all Única, were greater in all application intervals. The low yields in Única are remarkable, as well as the immense yield increase in Betina achieved by fungicide application every 4 days. In varieties with susceptibility level 6 a fungicide application interval of 4 days was the only treatment that provided satisfactory protection and generated high yields. An application interval of 8 days significantly reduced the yield. Application intervals of 12 days and more did not provide sufficient protection against late blight.



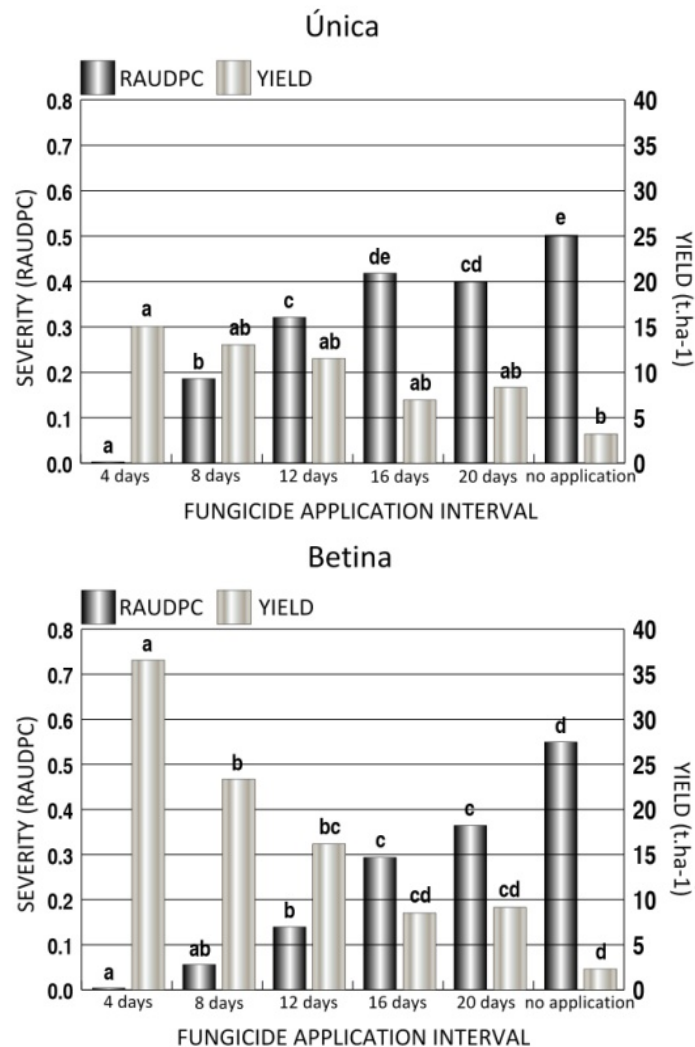


Figure 11. Averages and Tukey values (5%) for severity and yield (t.ha-1) for five different application intervals and control treatment in I-Fripapa, Carolina, Única and Betina (susceptibility level 6).

3.2.4 Varieties with susceptibility level 7

Roja Nariño and Superchola were evaluated as very susceptible to potato late blight (Table 4). They showed a great difference in protection between different intervals of fungicide application. Only an interval of 4 days gave a satisfactory protection throughout the growing season, as shown in Figure 12. An interval of 8 days provided protection during 80 days, but thereafter the area of affected foliage increased to between 20 and 50%. The effect of the increased disease on the harvest depends on which level the plants had reached when the increase began. Application intervals of 12, 16 and 20 days hardly provided any protection against late

blight; the plants were affected to almost the same extent as the control plants, the only difference being that in some cases the increase started 10 days later in parcels where fungicides were applied. Once the epidemic started to increase it grew relentlessly; after about 40 days approximately 80% of the foliage wilted and after 126 days the entire plants were dead.

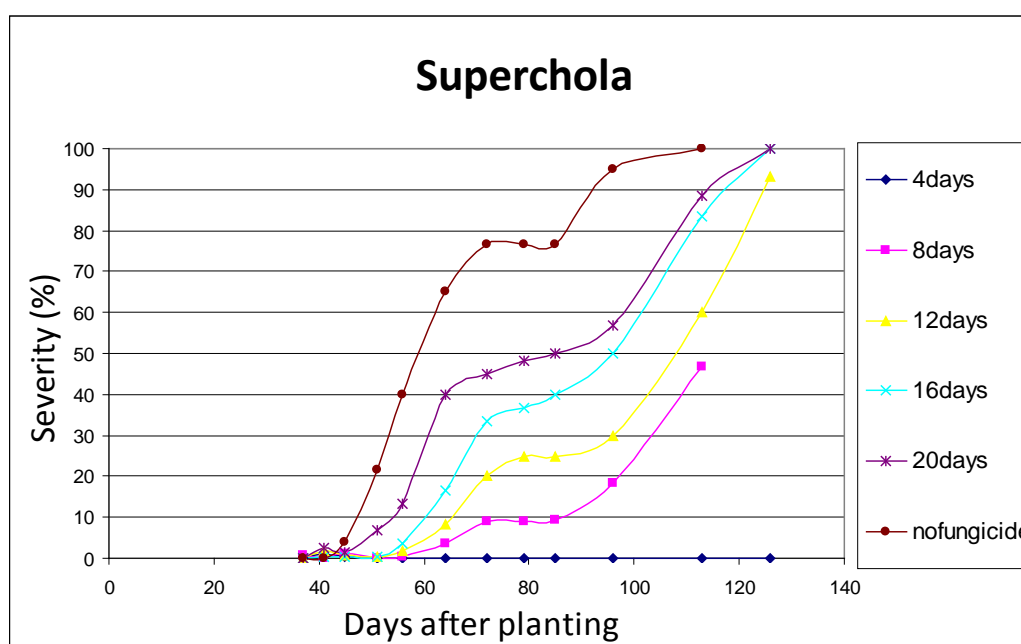
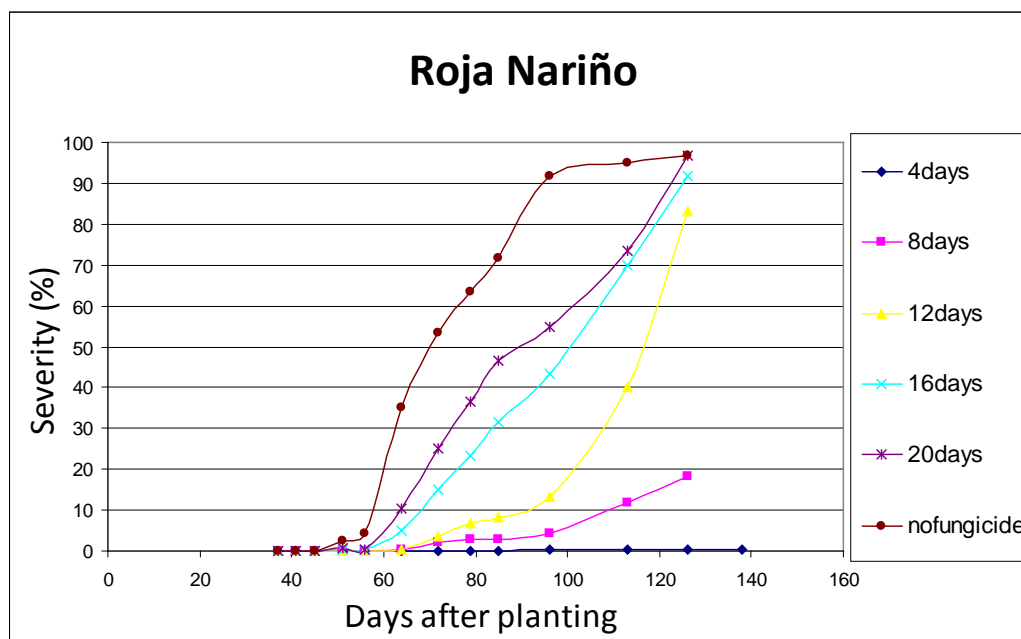


Figure 12. Development of late blight epidemic in varieties of susceptibility level 7 (Roja Nariño and Superchola) with different intervals of fungicide application.

The highest yields in the varieties Roja Nariño and Superchola were generated when fungicides were applied every 4 days (Figure 13). With fungicide application every 8 days the yield was significantly reduced (close to 10 tonnes/ha). Still

the yields generated with fungicide application every 8 days were twice as high as the yields generated by longer application intervals. The yields obtained with fungicide application every 12, 16 and 20 days were considerably minor and possibly not even economically viable. In varieties with susceptibility level 7 applications of fungicides every 4 days guaranteed satisfactory protection against late blight. Higher intervals implied decreased yield and greater risk for economic losses for the farmers.

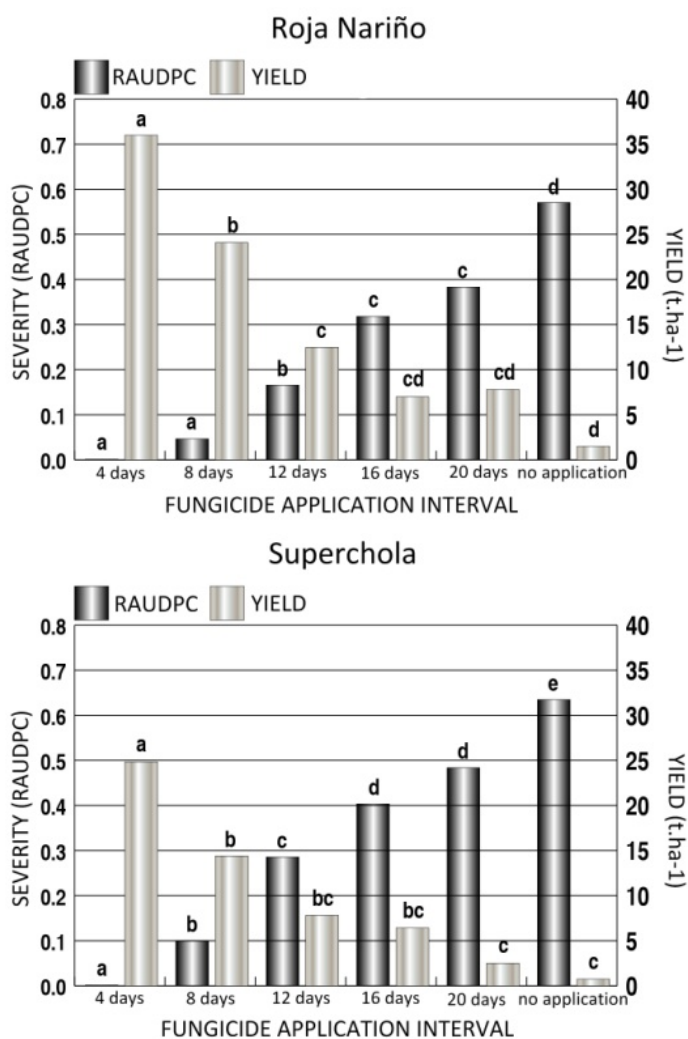


Figure 13. Averages and Tukey values (5%) for severity and yield (t.ha-1) for five different application intervals and control treatment in Roja Nariño and Superchola (susceptibility level 7).

3.2.5 Varieties with susceptibility level 8

The most susceptible varieties were I-Gabriela and Cecilia (Table 4). Their curves were similar to the curves exhibited by the varieties with susceptibility level 7 (Figure 14). However, in the varieties with susceptibility level 8 treatments with application intervals 12, 16 and 20 days stopped to be protective after 56 days, and in all treatments the area of affected foliage reached 100% within 113 days. Treatment with 8 days application interval stopped being effective after 96 days and after another 30 days the disease severity reached 40%.

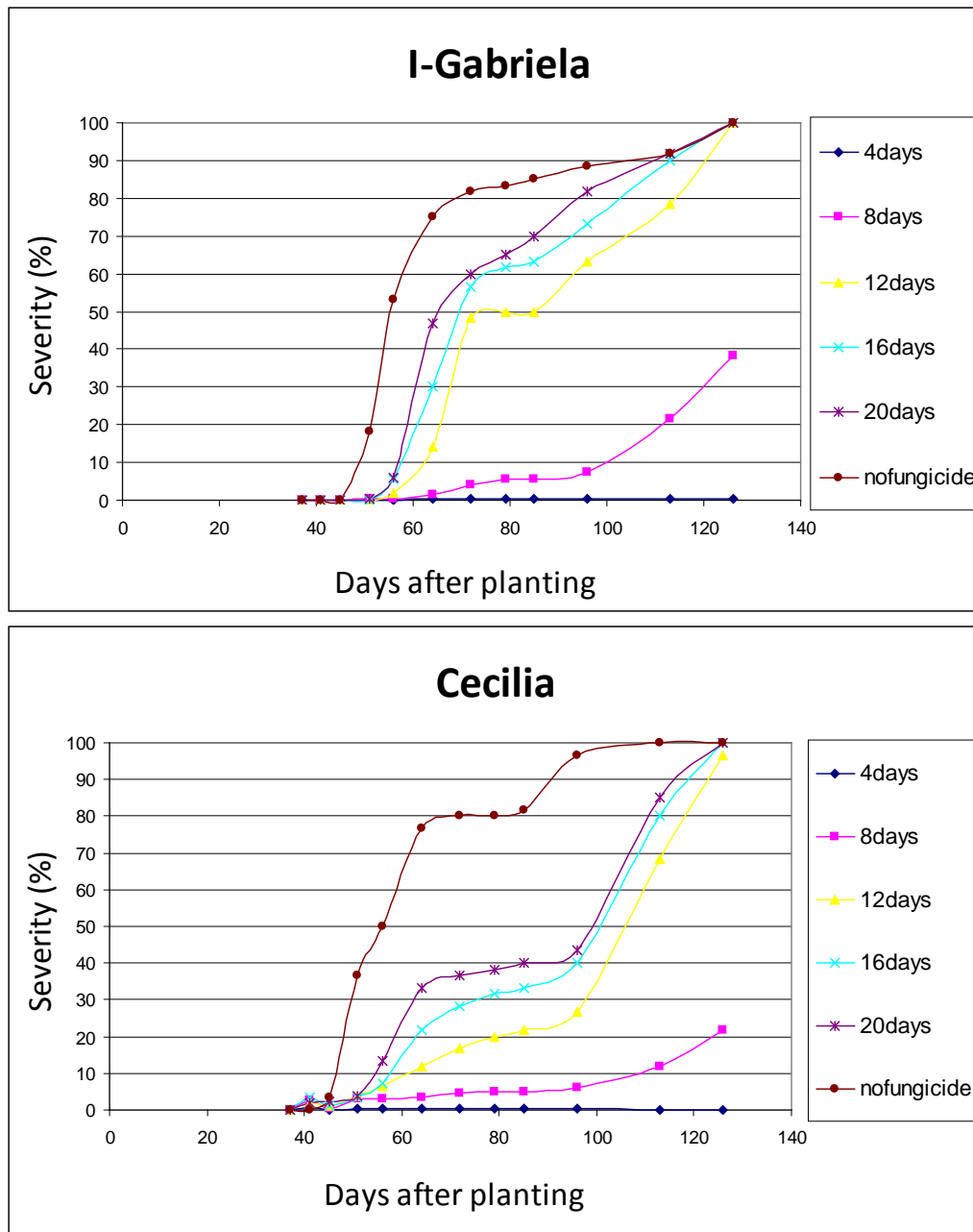


Figure 14. Development of late blight epidemic in varieties of susceptibility level 8 (I-Gabriela and Cecilia) with different intervals of fungicide application.

The high susceptibility to late blight in these varieties implies that the level of protection is insignificant for treatments with fungicide application intervals of 12, 16 and 20 days (Figure 15). These application intervals gave a yield that barely exceeded the national mean yield (10 tonnes/ha). An application interval of 8 days

generated yields of 22 tonnes/ha. Only an interval of 4 days generated a yield of 30 tonnes/ha, which corresponds to the capacity of these varieties, according to the breeding companies (Taípe, pers.com., 2010).

In varieties with susceptibility level 8 an application interval of 4 days was the only treatment that assured a sufficient yield for the farmers. An application interval of 8 days reduced the yield with 8 to 12 tonnes/ha, and implicates a great risk for economic losses.

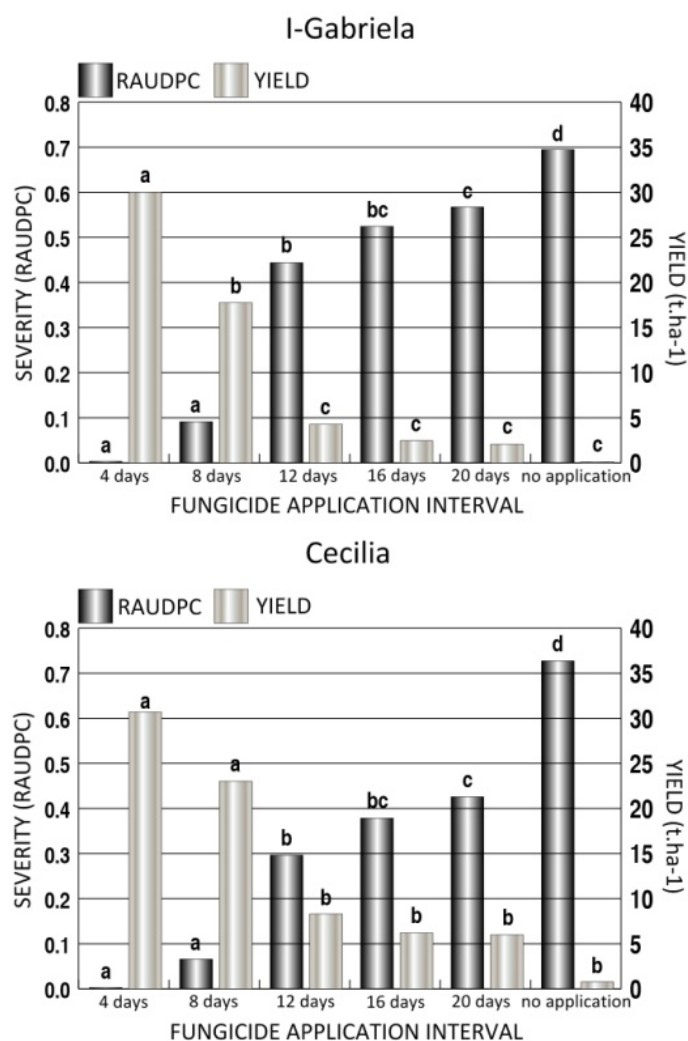


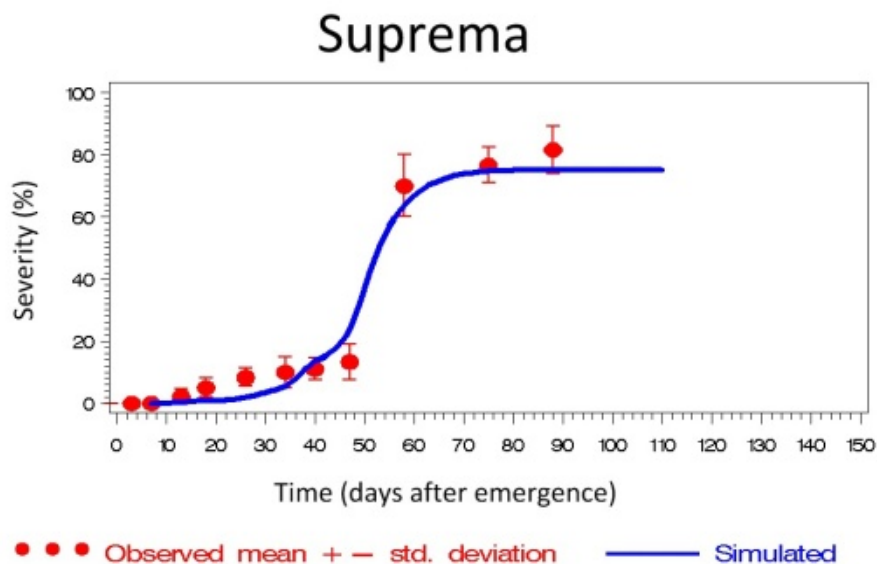
Figure 15. Averages and Tukey values (5%) for severity and yield (t.ha-1) for five different application intervals and control treatment in I-Gabriela and Cecilia (susceptibility level 8).

3.2.6 Conclusions

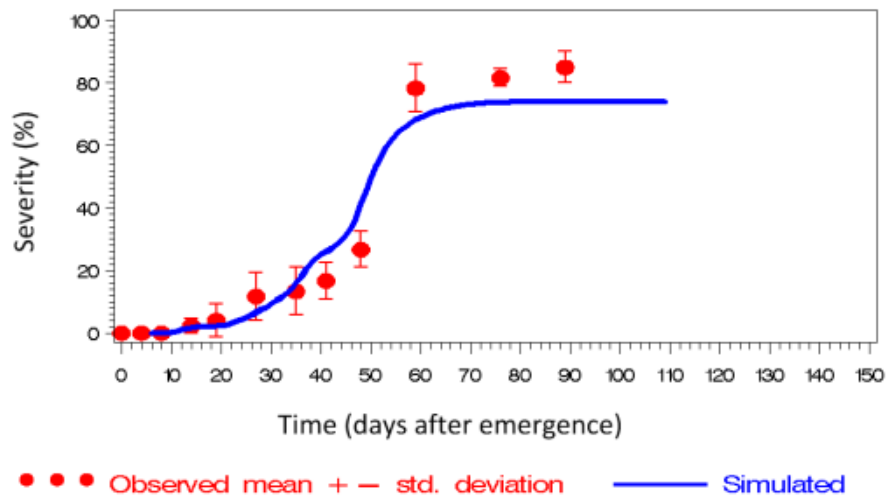
Varieties with a susceptibility level of 4 or 5 were successfully protected against yield losses due to potato late blight with application intervals up to 16 days. However, in varieties with susceptibility level 5 treatments with fungicide application every 12 days significantly reduced the yield. Varieties with susceptibility level 6 were successfully protected against epidemics of late blight with application intervals up to 8 days, although shorter interval (4 days) gave increased yield. In varieties with susceptibility levels of 7 and 8 only application intervals of 4 days gave efficient protection against potato late blight. Thus, the least susceptible cultivars (most resistant ones) could deliver reasonable yields with fungicide application intervals up to 16 days. The minimum interval then decreased with increasing susceptibility (decreasing resistance), and the most susceptible cultivars (with susceptibility levels of 7 and 8) could only deliver reasonable yields with frequent applications (4 day intervals).

3.3 Validation of computer simulation

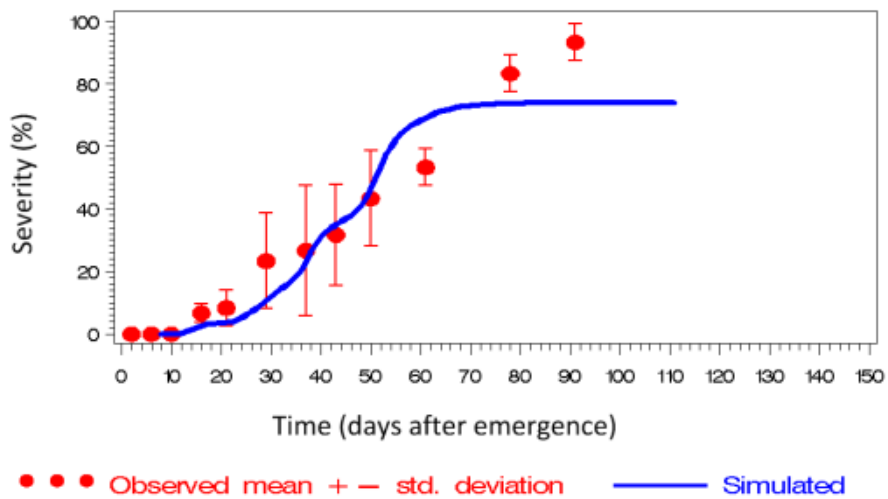
Computer model simulations produced by LATEBLIGHT were compared with the epidemic development of late blight in the different cultivars observed in the field trial. These comparisons show that the general level of agreement between simulated and observed epidemics was high (Figure 16).



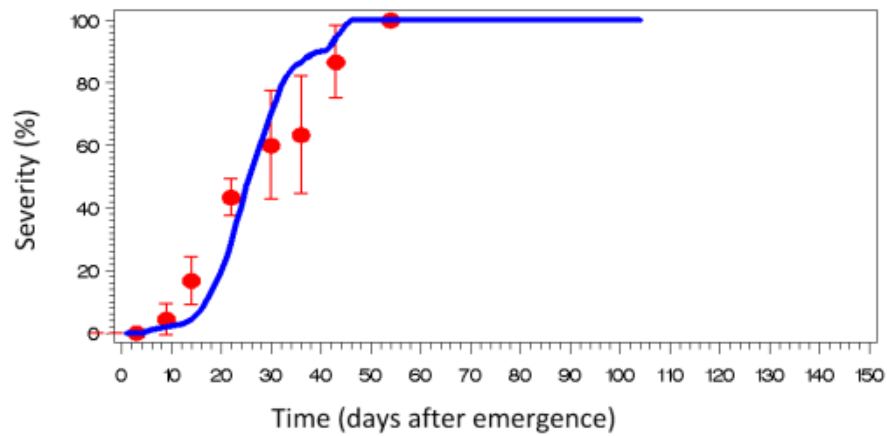
I-Estela



I-Natividad

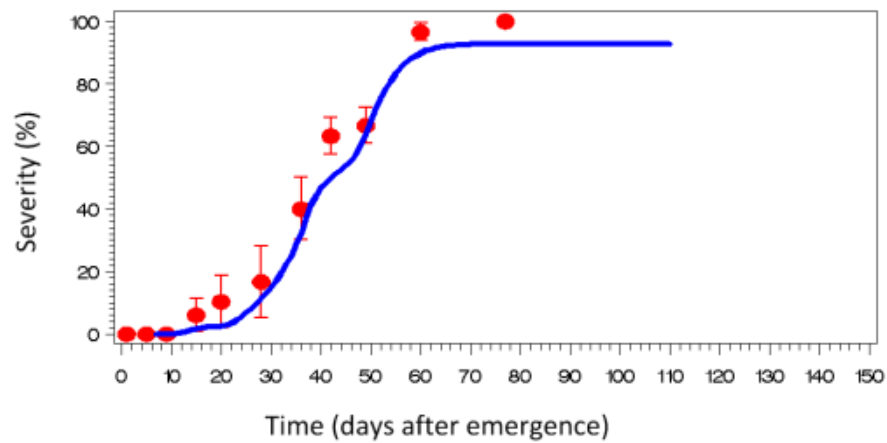


Nova



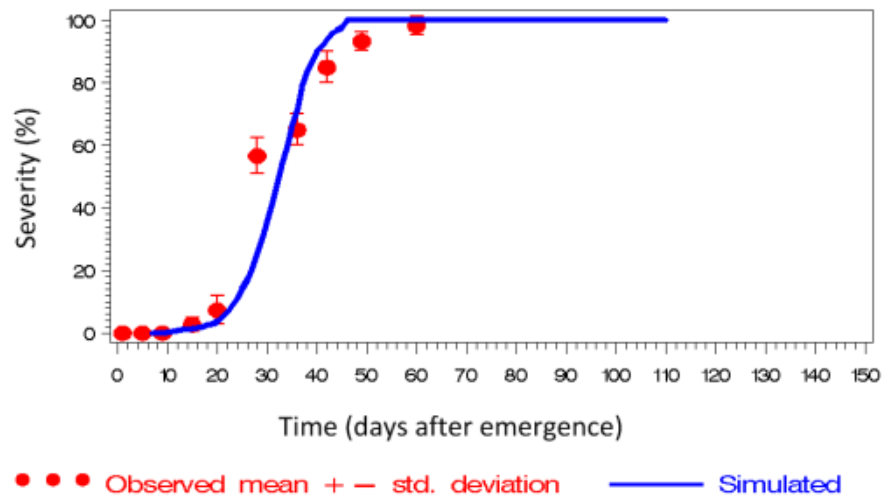
• • • Observed mean + — std. deviation — Simulated

I-Fripapa

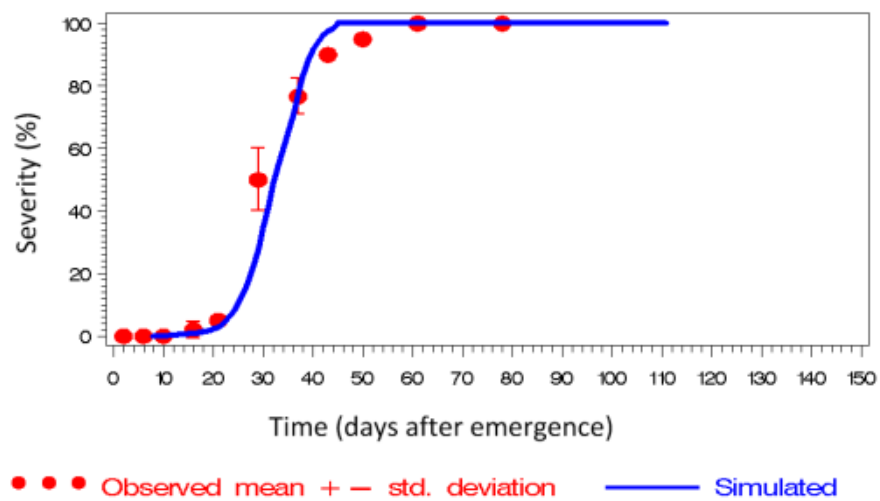


• • • Observed mean + — std. deviation — Simulated

Carolina



Única



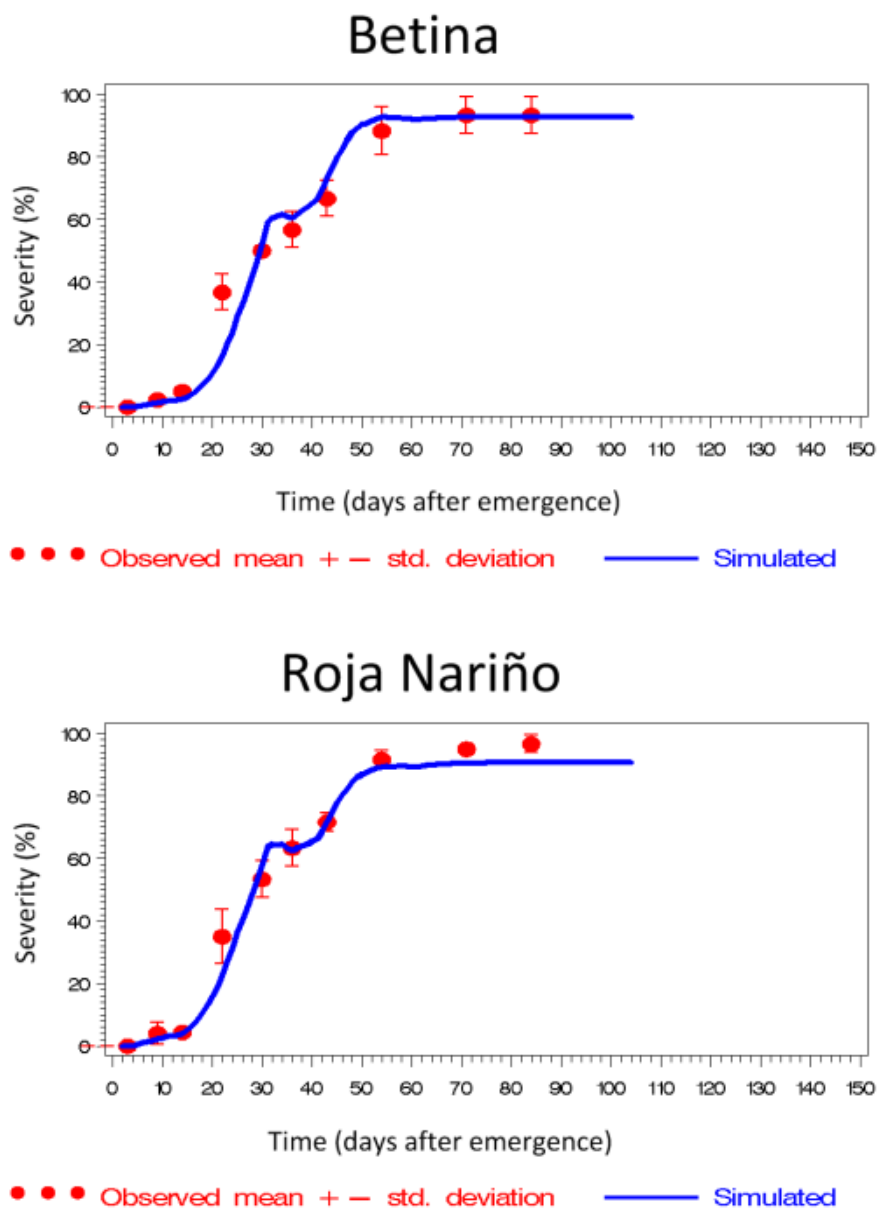
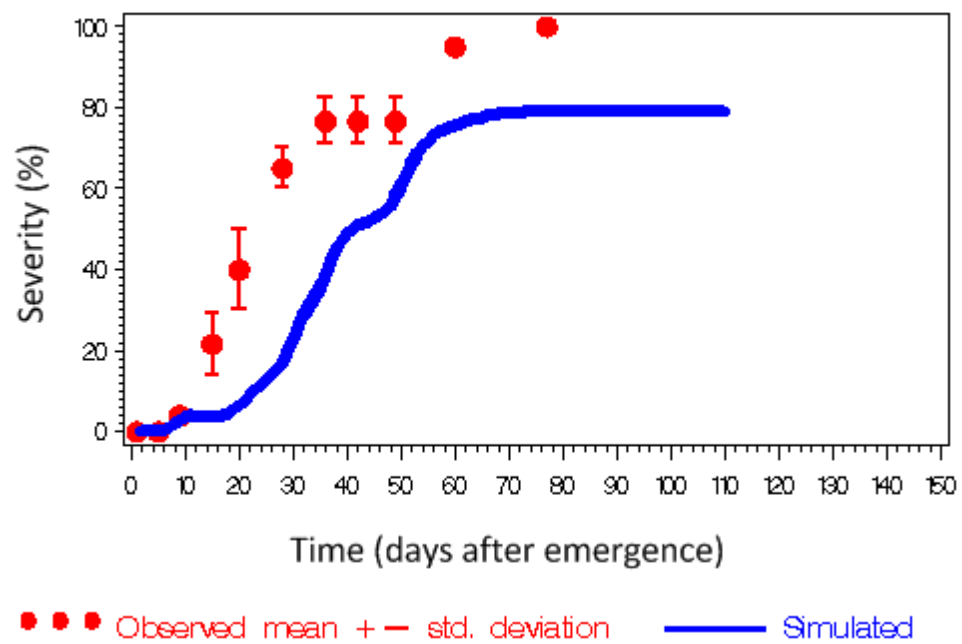


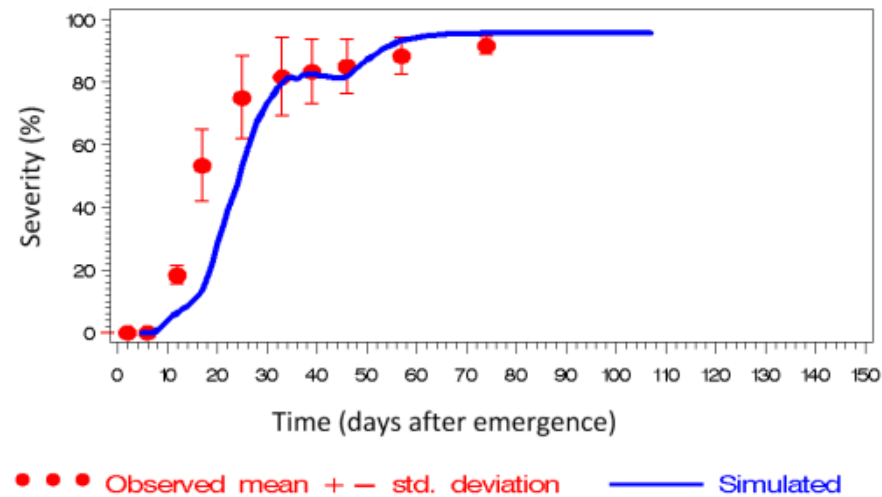
Figure 16. Comparison of development of potato late blight in 9 different cultivars in computer simulation and observed epidemics in field trial

The simulated epidemics for Superchola, I-Gabriela, and Cecilia were somewhat delayed compared to the observed data (Figure 17). These varieties were at the more susceptible end of the scale and the parameters for these more susceptible cultivars might need smaller amounts of adjustment in order to duplicate the results of the field experiments.

Superchola



I-Gabriela



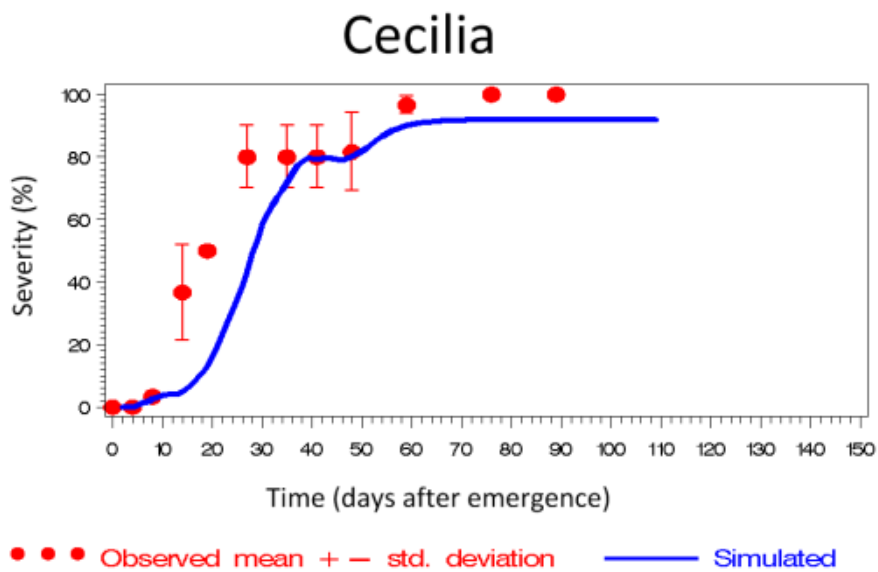


Figure 17. Comparison of development of potato late blight in 3 different cultivars in computer simulation and observed epidemics in field trial

3.3.1 Conclusions

According to this validation the computer model LATEBLIGHT provides trustworthy simulations of epidemics of late blight in the Andes. Minor adjustment might be required for the more susceptible cultivars, but this validation is only a single season and more epidemics are needed in order to confirm this.

4 Discussion

4.1 Quantification of resistance to *Phytophthora infestans*

By means of field trial the varieties were successfully evaluated according to the scale of Yuen and Forbes (2009). Usage of cultivars with low susceptibility to *P. infestans* is one measure to control late blight and severe economic losses (Andrade-Piedra et al., 2005), and approved evaluation of commonly used varieties is therefore important. If, or when, this information is conveyed to local farmers it might change current production patterns and result in an increased cultivation of potato varieties with a higher level of resistance.

It is noticeable that the resistance levels differed from the levels of resistance estimated beforehand. Some of the varieties that were previously considered to be resistant to late blight were evaluated as susceptible in this trial, i.e. I-Gabriela and Superchola, while varieties that were considered to be susceptible were evaluated as resistant, i.e. I-Estela and Pastusa Suprema (Table 1 and 4). In some cases there was a great difference between varieties that are usually considered to be of equal level of susceptibility. Pastusa Suprema, I-Natividad, Carolina and Roja Nariño are all considered as susceptible to late blight. However, in this trial Pastusa Suprema was evaluated as level 4, I-Natividad as level 5, Carolina was evaluated as level 6 and Roja Nariño as level 7. I-Fripapa is a variety that is widely cultivated in Ecuador and it is generally considered to be moderately resistant towards *P. infestans*, in this experiment however, it was evaluated as quite susceptible to the pathogen (Table 4). A possible explanation to this is that the prior estimations were unsatisfactory. This might be of major importance since e.g. European susceptibility evaluations cannot be applied in South America. The inconsistency shows the necessity to perform careful evaluations of different potato varieties based on the same scale to enable the possibility to compare the results. Another

explanation might be that the former evaluations were performed a long time ago. As resistance tends to change with time this could be a contributing factor to the differing results (Van der Plank, 1963). The scale of Yuen and Forbes (2009) has been adapted for potato varieties with general resistance to late blight. It is possible that some of the evaluated varieties have specific resistance to the disease, and this might be a reason for why the results of the evaluation differ from prior estimations of resistance. The current experiment was performed during one season on one single location. Hence, there could also be a variety of possible error sources due to climate and management. It is desirable to proceed with the susceptibility evaluation over the coming years in a variety of different locations in order to reach satisfactory results.

4.2 Relation between resistance and need for fungicide application

Successful disease management is a very important factor in order to increase productivity and reduce production costs for resource-poor farmers (Nelson et al., 2001). CIP is striving to develop easy to use decision-support systems and one part in this work is to quantify advisable amount of fungicide application levels for different varieties of potato. The evaluation of fungicide application need indicates that varieties with a lower susceptibility to late blight, such as Pastusa Suprema and I-Estela require less frequent applications than more susceptible varieties, such as I-Gabriela and Cecilia. This has also been shown in Norwegian experiments (Naerstad and Hermansen, 2010). There are major differences in application needs between the different varieties. Potato varieties with high susceptibility to late blight generally have a need for short application intervals in order to provide satisfactory yield. This constitutes a conflict between yield and economy for resource poor farmers.

This set of experiments represents only one growing season in Ecuador, and other trials in different locations and years are needed to confirm these results. These results, however, have a direct application in potato production, and one should inform local farmers in Ecuador about these differences between varieties and stress the importance of adequate usage of fungicides in potato production. It is also important to advise farmers to cultivate varieties with high level of resistance to the disease in order to reduce the total usage of fungicides.

4.3 Validation of computer simulation

The LATEBLIGHT computer model has been modified so that it can be used in the Andes by Andrade-Piedra et al. (2005a). The results of this project indicate that there is a high level of agreement between simulated and observed epidemics of late blight, which is cohesive with prior results from validation of the model in Peru (Andrade-Piedra et al. 2005b). These indications are very positive since the usage of computer model simulations instead of laborious field trials is likely to save a lot of time and money in future crop breeding programs and evaluations of different management practices.

References

Literature

- Andrade-Piedra, J. L., Hijmans, R., Forbes, G., Fry, W., Nelson, R. (2005a). Simulation of Potato Late Blight in the Andes, I: Modification and Parameterization of the LATEBLIGHT Model. *Phytopathology* 95, 1191-1199
- Andrade-Piedra, J. L., Hijmans, R., Juárez, H., Forbes, G., Shtienberg, D., Fry, W. (2005b). Simulation of Potato Late Blight in the Andes, II: Validation of the LATEBLIGHT model. *Phytopathology* 95, 1200-1208
- Andrade-Piedra, J. L. (2006). *POLUX- Potato Late Blight Simulator version 1.0, User's manual*. International Potato Center, Lima, Peru
- Andersson, B., Sandström, M. (2000). *Bladmögel och brunröta på potatis*. Faktablad om växtskydd, Sveriges lantbruksuniversitet, Uppsala
- Andersson, B., Widmark, A-K., Yuen, J., et al. (2009). The role of oospores in the epidemiology of potato late blight. *Proceedings of the III International Late Blight Conference, Beijing, China*, April 3-6 2008. *Acta Horticulturae* 834
- Bruhn, J.A. and Fry, W.E. 1981. Analysis of potato late blight epidemiology by simulation modeling. *Phytopathology* 71: 612-616.
- Cáceres, P., Pumisacho, M., Forbes, G., Andrade-Piedra, J. L. (2008). *Learning to control potato late blight- A facilitator's guide*. International Potato Center, Lima, Peru
- Cole, D., Sherwood, S., Crissman, C., Barrera, V., Espinosa, P. (2002). Pesticides and Health in Highland Ecuadorian Potato Production: Assessing Impacts and Developing Responses. *International Journal of Occupational and Environmental Health* 8, 182-190
- Forbes, G., Escobar, X., Ayala, C., Revelo, J., Ordoñez, M., Fry, B., Doucett, K., Fry, W. (1997). Population Genetic Structure of *Phytophthora infestans* in Ecuador. *Phytopathology* 87, 375-380
- Forbes, G.A., Fry, W.E., Andrade-Piedra, J.L., and Shtienberg, D. 2008. Simulation Models for Late Blight Management and Ecology. In: Ciancio, A. and Mukerji, K.G. (editors). *Integrated Management of Diseases Caused by Fungi, Phytoplasma, and Bacteria*. Springer, 419 pp.
- Govers, F., Meijer, H.J.G., Ha Tran, Wagemakers, L., Raaijmakers, J.M. (2009). Unraveling the Senses of *Phytophthora*; Leads to Novel Control Strategies? *Proceedings of the III International Late Blight Conference, Beijing, China*, April 3-6 2008. *Acta Horticulturae* 834
- Harris, P. (1992). *The Potato Crop*. London: Chapman & Hall
- Henfling, J. W. (1987). *El Tizón Tardío de la Papa: Phytophthora infestans*. Boletín de Información Técnica 4. Centro Internacional de la Papa, Lima, Peru

- Kamoun, S., van West, P., Govers, F. (1998). Quantification of late blight resistance of potato using transgenic *Phytophthora infestans* expressing β -glucuronidase. *European Journal of Plant Pathology* 104, 521-525
- Kromann, P., Taïpe, A., Perez, W., Forbes, G. (2009). Rainfall thresholds as support for timing fungicide applications in the control of potato late blight in Ecuador and Peru. *Plant Disease* 93, 142-148
- Mancero, L. (2007). *Potato Chain Study – Analysis of the Potato Productive Chain in Ecuador, 3 case studies*. FAO.EASAE-CIP Project
- Naerstad, R., and Hermansen, A. (2001). *Reduced fungicide input in late blight control. (REDUCE 2007-2011) Preliminary results from 2001 to 2009*. PPO-Special Report no 14:193-198
- Nelson, R., Orrego, R., Ortiz, O., Mundt, C., Fredrix, M., Vinh Vien, N. (2001). Working with Resource-Poor Farmers to Manage Plant Diseases. *Plant Disease* 85
- Oyarzún, P., Garzón, C., Leon, D., Andrade, I., Forbes, G. (2005). Incidence of Potato Tuber Blight in Ecuador. *American Journal of Potato Research* 82, 117-122
- Pérez, W., Forbes, G. (2008). *El tizón tardío de la papa, Manual Técnico*. Centro Internacional de la Papa, Lima, Peru
- Quinn, G.P., and Keough, M.J. 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, UK. 537 pp.
- Umaerus, V. and Umaerus, M. (1994). *Inheritance of resistance to late blight*. In: Bradshaw JE. and Mackay GR. (eds) *Potato Genetics* (365-401) CAB International, Wallingford UK
- Van der Plank, J. E. (1963). *Plant Diseases: Epidemics and Control*. New York: Academic Press
- Wastie, RL. (1991). *Breeding for resistance*. In: Ingram DS and Williams DS (eds). *Phytophthora infestans, the Cause of Late Blight of Potato. Advances in Plant Pathology*, vol 7 (193-224). Academic Press Ltd, London
- Wesseling, C., Corriols, M., Bravo, V. (2005). Acute Pesticide Poisoning and Pesticide Registration in Central America. *Toxicology and Applied Pharmacology* 207, 697-705
- Yuen, J., Forbes, G. (2009). Estimating the level of susceptibility to *Phytophthora infestans* in potato genotypes. *The American Phytopathological Society, Phytopathology* 99

Electronic documents

- American Phytopathological Society. (2011). The Irish Potato Famine and the Birth of Plant Pathology. [online] (2011). Available from: <http://www.apsnet.org/publications/apsnetfeatures/Pages/PotatoLateBlightPlantDiseasesComponents.aspx> [2011-06-10]
- Andersson B., Widmark A-K. (2008). Fakta om potatisbladmögel [online] (2009-03-18). Available from: <http://www.slu.se/?id=551&puff=203> [2009-09-15]
- Environmental Protection Agency, USA (2005). Mancozeb Facts. Prevention, Pesticides and Toxic Substances. [online] (2005-09). Available from: http://www.epa.gov/oppsrrd1/REDs/factsheets/mancozeb_fact.pdf [2011-05-07]
- FAO (2008). International Year of the Potato 2008. The global potato economy. [online] (2008). Available from: <http://www.Potato2008.org/en/potato/IYP-3en.pdf> [2011-05-05]
- International Potato Center (2006). Home page. [online] (2006). Available from: <http://www.cipotato.org/potato/facts/growth.asp> [2009-09-15]
- International Potato Center (2010). Research/Combating Late Blight [online] (2010). Available from: http://www.cipotato.org/research/projects/pf01_lateblight.asp [2010-05-10]

Oyarzún, P., Taipe, A, Forbes, G. (2001). *Phytophthora infestans* characteristics and activity in Ecuador [online] (2001). Available from:
<https://research.cip.cgiar.org/confluence/display/GILBWEB/Ecuador> [2010-05-15]

Personal Communication

Forbes, G. International Potato Center, Lima, Peru. Personal communication. September 2009

Taipe, A. International Potato Center, Quito, Ecuador. Personal communication. May 2010

Acknowledgement

This thesis was supported by the Minor Field Study (MFS) scholarship from the Swedish International Development Cooperation Agency (SIDA). The study was performed in Quito, Ecuador at the research center of Centro Internacional de la Papa. I would like to thank Arturo Taipe and Professor Jonathan Yuen, my supervisors in Ecuador and Sweden, and Greg Forbes for giving me the opportunity to go to Ecuador and for their help with the project and during the writing process. I would also like to thank all the co-workers at CIP, Quito for their helpfulness and assistance during my stay in Ecuador.