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Evaluation of breeding strategies for resistance and tolerance to late blight in potato by means of simulation

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Abstract

A field experiment with three potato cultivars, where plants were inoculated with *Phytophthora infestans*, was used to parameterize a model of potato growth and blight population dynamics. The model was validated by accurately simulating a field experiment conducted in another year. Sensitivity analysis with the model showed that late cultivars are longer able to maintain a green canopy in the presence of disease, but still suffer more yield loss than early cultivars. The level of partial resistance of a cultivar was more important than its level of tolerance, and other plant characteristics. The model calculations showed that only between 4 and 15% of the yield loss in the experiments was due to accelerated leaf senescence caused by the disease; the major part of the loss was caused by lesion coverage of leaves.

Additional keywords: *Phytophthora infestans*, accelerated senescence, light interception, yield, model.

Introduction

Yield loss caused by *Phytophthora infestans* (Mont.) de Bary varies between potato cultivars. The variation is caused by different growth rates of the pathogen populations and by differences in crop response to infection. In two previously reported field experiments, carried out in 1987 and 1988 (Van Oijen 1991a, 1991b) with three cultivars, differing in maturity class and level of partial resistance, measurements were made of seasonal courses of foliage growth and senescence, coverage of leaves by blight lesions, and tuber yield. These measurements were used in the present study to explain the differences in yield loss between the cultivars, and to identify the major plant characteristics which affect yield loss. To achieve these goals a simple simulation model was constructed, that includes the growth of both the host crop and the pathogen population. Data of the 1987 experiment were used to estimate parameter values for the model, the remaining data were used for model validation. The model was subjected to a sensitivity analysis, in which the effect of changing different plant characteristics on yield loss was assessed.

Model structure and parameterization

The model was constructed by combining the potato crop growth model LINTUL (Spitters and Schapendonk, 1990) and the late blight population dynamics model BLIGHT (Van Oijen, 1989). The essential features of these models are given below.

Crop growth in LINTUL is linearly related to light interception, which has an asymptotic relationship with the Leaf Area Index (*LAI*). The partitioning of growth between leaves, stems, roots and tubers is governed by the developmental stage of the crop, which is calculated from the temperature sum (°C d) and the maturity class of the cultivar. Early cultivars initiate tuber growth at a lower temperature sum than late cultivars, at the expense of foliage and root growth. Leaf area is calculated by multiplying leaf weight with a constant Specific Leaf Area (*SLA*).

The growth of the pathogen population is modelled as spatially homogeneous in BLIGHT. Only lesions on leaves are considered because stem lesions had a negligible effect on leaf loss (Van Oijen, 1991b). The density of leaf lesions and their size distribution change dynamically. These processes are controlled by the amount of available host leaf area and by five parameters: infection efficiency (*IE*), latent period (*LP*), lesion growth rate (*LG*), sporulation intensity (*SI*) and infectious period (*IP*). These parameters, which determine the level of partial resistance of a cultivar, are called 'resistance components'.

Tolerance is the ability to endure the presence of a pathogen with reduced disease symptoms and/or damage (Parlevliet, 1979). Potato cultivars show intolerance to blight in that the presence of the fungus in some parts of the foliage increases the rate of senescence in uninfected parts (Van Oijen, 1991b). This acceleration of leaf senescence due to the disease is included in the model. At any time during the epidemic, disease severity, expressed as the percentage of leaf area covered with lesions, is assumed to cause an equal percentage of leaf senescence in the *non-lesion covered* leaf area (Van Oijen, 1991b).

Leaf lesion coverage and accelerated leaf senescence due to late blight start in the bottom leaf layers and gradually move upwards in the canopy (Lapwood, 1961; Van Oijen, 1991b). Therefore blight reduces total light interception mainly by reducing the area of green leaves and not by shadowing green leaves by lesion-covered or senesced leaves. The Light Use Efficiency (*LUE*), which relates crop biomass to the amount of light intercepted by green leaf area, is not reduced by the disease, so in this respect potatoes are completely tolerant to blight (Haverkort and Bicamumpaka, 1986; Van Oijen, 1991a). Therefore the interaction of host and parasite is modelled simply by calculating the dynamics of loss of green leaf area caused by pathogen population growth and accelerated leaf senescence.

In the experiments used for model parameterization and validation, epidemics were initiated artificially by spraying inoculum over plots about one month after emergence. The model thus assumes homogeneous input of inoculum on the date of inoculation (Table 1).

The experiments were done with three cultivars: the early susceptible cv. Bintje, the early resistant cv. Surprise and the late resistant cv. Pimpernel. In the simulations these three cultivar types and a hypothetical late susceptible one were examined. Cultivar earliness or lateness was parameterized by a maturity class of 6.5 or 3.5, respectively (Spitters and Schapendonk, 1990). This causes the late cultivars to show a marked

Table 1. Complete listing of model parameter values and inputs that were different for simulations of different cultivars (early/late, susceptible/resistant) or years (1987/1988).

Maturity class:		
Onset of tuber filling (°C d)	Early: 150.7	Late: 234.5
Leaf senescence rate	[1]	[1]
Level of partial resistance:		
Infection efficiency (*IE*, %)	Susc.: 2.4	Res.: 1.2
Lesion growth rate (*LG*, m d^{-1})	Susc.: 0.003	Res.: 0.0015
Year:		
Seasonal course of temperature	1987: measured daily	1988: measured daily
Seasonal course of light	1987: measured daily	1988: measured daily
Date of inoculation	1987: June 23	1988: July 27
Inoculum density (sporangia m^{-2})	1987: 4×10^6	1988: 4×10^7
Light use efficiency (*LUE*, g MJ^{-1})	1987: 2.95	1988: 2.35
Maturity class × *Year:*		
Date of emergence (early cvs)	1987: May 19	1988: June 18
Date of emergence (late cvs)	1987: May 23	1988: June 24

[1] The relation between leaf senescence rate and the actual temperature, the temperature sum and the maturity class was given by Spitters and Schapendonk (1990).

delay in tuber filling in favour of foliage growth (Jones and Allen, 1983).

The level of cultivar resistance was parameterized by means of the resistance components. These were not measured in the experiments. The component parameters of susceptible cultivars were assumed to have the most 'susceptible' values reported in the literature listed by Van Oijen (1989). For the resistant cultivars the values of *IE* and *LG* were set 50% lower, which is still in the range of observed genetic variation for these components (Table 1). The model parameters that represent the *LAI* at emergence and the efficiency of inoculum dispersal were also not assessed in the experiments. These parameters were set at values that caused the best agreement between simulations and measurements of host leaf area dynamics and pathogen population growth in cvs Bintje and Pimpernel in the 1987 experiment (Exp. 1 in Van Oijen, 1991a). Although in 1988 planting was much delayed (1 June 1988 vs. 29 April 1987), leading to a shorter growing season and lower yields, the 1988 experiment was simulated with the parameter values derived for the 1987 experiment. Only inoculum density was set ten times higher, to account for better infection conditions at the day of artificial inoculation in 1988 because of previous sprinkler irrigation, and the *LUE* was lower, in accordance with the experimental results (Van Oijen, 1991a) (Table 1).

Model validation

Experimental data for the seasonal courses of percentage ground cover by green leaves, averaged over the cultivars, have been presented earlier (Van Oijen, 1991a). For ease of comparison with simulation results the data for the inoculated and control treatments of the separate cultivars are shown here (1987: Fig. 1A; 1988: Fig. 1B). In 1987, ground cover in the controls decreased earliest in the early cvs Bintje and Surprise,

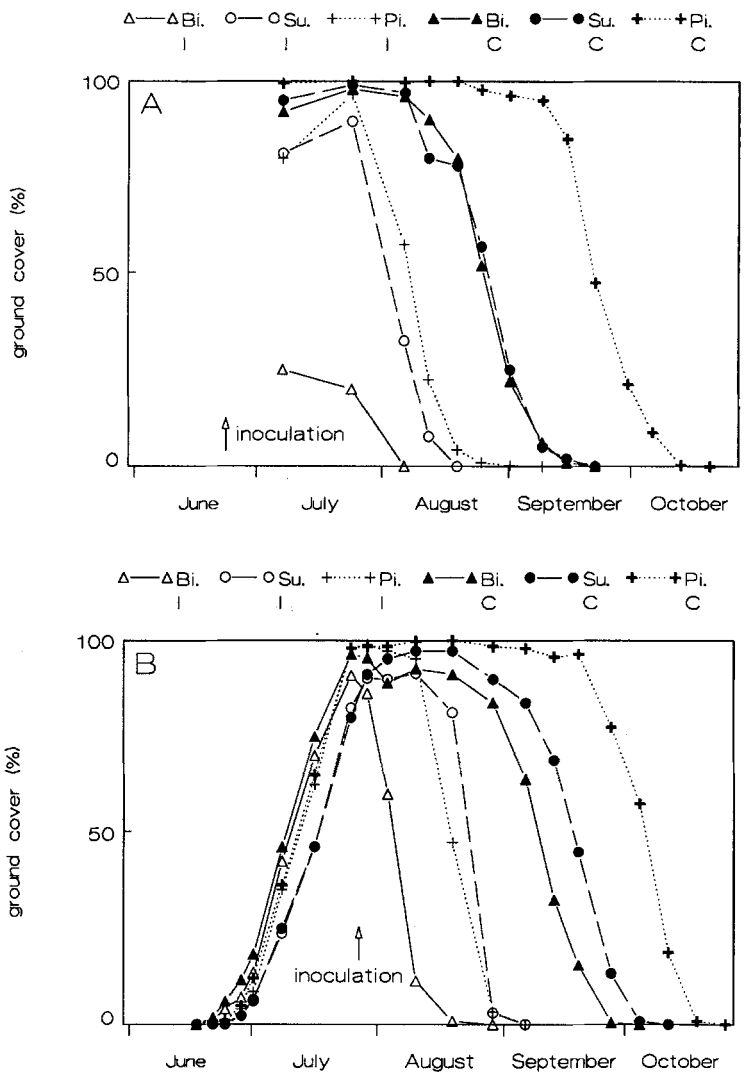

Fig. 1. Measured and simulated time courses of ground cover in inoculated (I) and control (C) plots of the susceptible early cv. Bintje (Bi), the resistant early cv. Surprise (Su), the resistant late cv. Pimpernel (Pi) and a hypothetical susceptible late cultivar (SL). Note: only the maturity class affects the simulated time courses in control plots, lines for susceptible and resistant cultivars fall together. A: Measurements 1987; B: Measurements 1988; C: Simulations 1987; D: Simulations 1988.

while in the inoculated plots the blight susceptibility of cv. Bintje caused an early foliage death (Fig. 1A). Results were similar in 1988, except that cv. Surprise slightly outlasted cvs Bintje and Pimpernel in the control and inoculated treatments, respectively (Fig. 1B).

Seasonal courses of ground cover, light interception during the growing season and final tuber yield were simulated very well for both experiments (Figs 1C and 1D; Table

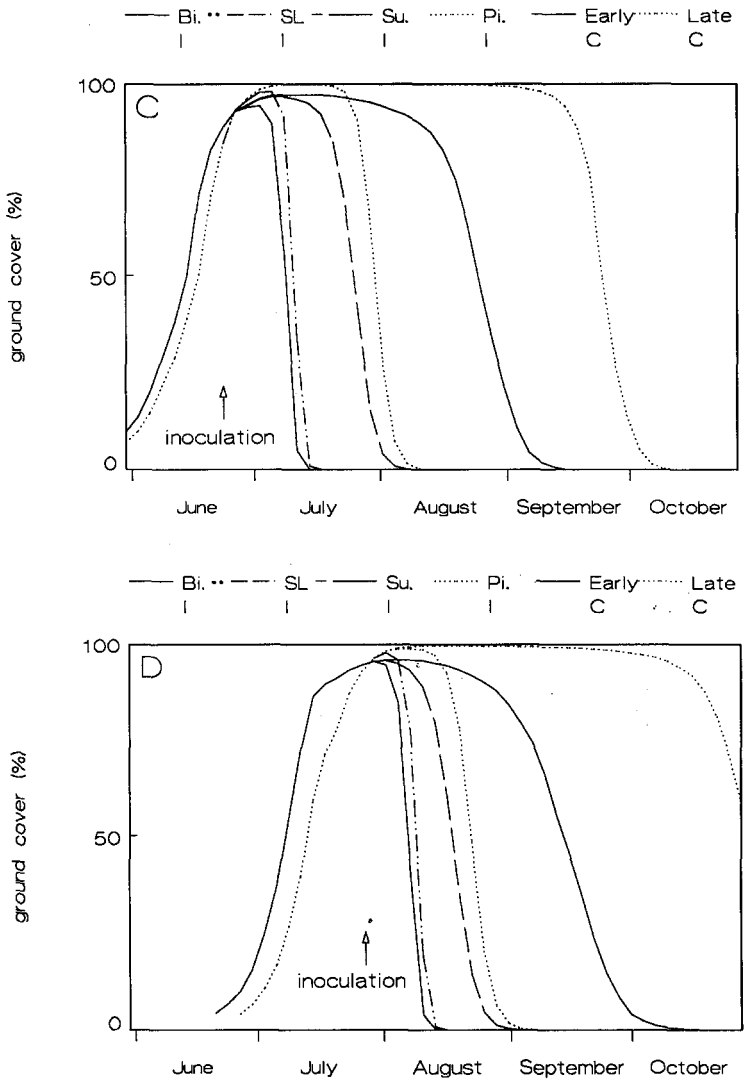

Fig. 1. (Continued.)

2). A regression analysis on the data of light interception and yield that had not been used for model parameterization, i.e. the 1987 data of cv. Surprise and all 1988 data (Table 2), showed that the simulations accounted for most of the variance between measurements ($r^2 = 0.96$, $n = 8$). The slope and intercept of the regression lines did not deviate significantly from unity and zero, respectively (F-test: $P = 0.10$ for light interception and $P = 0.09$ for yield), which indicates a high goodness-of-fit of the model (Dent and Blackie, 1979).

There were two exceptions to the general good agreement between simulations and measurements. Tuber yield of the control plots of cv. Surprise was overestimated in 1987, in spite of an accurate value for cumulative light interception (Table 2), and the

Table 2. Comparison of cumulative light interception (*PARCUM*) and yield of tuber dry matter in field measurements and simulations.

Year	Cultivar	Treatment	*PARCUM* (MJ m^{-2})		Yield (t ha^{-1})	
			measured	sim.	measured	sim.
1987	Susc./Early [1]	Control	530	520	11.8	11.5
		Inoculated	240	210	2.9	2.9
	Susc./Late	Control		670		13.9
		Inoculated		220		1.8
	Res./Early [2]	Control	510	520	9.5	11.5
		Inoculated	360	340	5.3	6.4
	Res./Late [3]	Control	670	670	14.0	13.9
		Inoculated	400	360	4.7	4.9
1988	Susc./Early [1]	Control	400	450	7.8	7.9
		Inoculated	170	210	2.0	2.4
	Susc./Late	Control		550		9.0
		Inoculated		190		1.2
	Res./Early [2]	Control	400	450	7.7	7.9
		Inoculated	270	300	4.2	4.4
	Res./Late [3]	Control	500	550	8.7	9.0
		Inoculated	280	300	3.2	3.0

[1] Measured data for cv. Bintje.
[2] Measured data for cv. Surprise.
[3] Measured data for cv. Pimpernel.

length of the 1988 growing season of late cultivars in the absence of disease was overestimated (compare the results for control plots of cv. Pimpernel in Figs 1D and 1B), but yield was estimated well (Table 2).

Sensitivity analysis

The validated model was used to assess the influence of different plant characteristics and experimental conditions on yield loss. Data on model sensitivity to cultivar maturity class and resistance level have been presented in Table 2, while data on the influence of other characteristics and conditions are listed in Table 3.

Maturity class and partial resistance. Lateness leads to a slightly longer period of maximum ground cover in blighted crops, both for resistant and susceptible cultivars, although resistance is the more important trait for prolonging the growing season (Figs. 1C, 1D). Yield, on the other hand, is lowest in blighted late cultivars, because of a later onset of tuber filling (Table 2).

Growth characteristics. Changing plant growth characteristics generally has little effect on yield of blighted crops (Table 3), except for increasing the relative rate of leaf

Table 3. Simulated tuber yields of blighted crops of four potato cultivar types, and their response to variation in plant characteristics and experimental conditions. Yields are expressed as percentages of the reference simulated yields for the inoculated treatment, averaged for 1987 and 1988 (Table 2). The multiplication factor was used to alter the specified parameters with respect to their value in the reference simulations.

	Multiplication factor	Susc. Early	Susc. Late	Res. Early	Res. Late
Reference yield (= 100%) (t ha^{-1})		2.66	1.49	5.41	3.98
Growth characteristics:					
1. Early leaf growth	1.2	115	111	112	108
2. Assimilate distribution	[1]	99	121	96	105
3. Specific leaf area (*SLA*)	1.2	107	108	107	106
4. Leaflet area	1.2	99	100	100	100
Tolerance component:					
1. Accelerated senescence	0	117	126	112	120
Resistance components:					
1. Lesion growth rate (*LG*)	0.8	115	124	115	121
2. Infection efficiency (*IE*)	0.8	108	112	108	111
3. Sporulation intensity (*SI*)	0.8	104	107	104	107
4. Latent period (*LP*)	1.2	104	106	103	104
5. Infectious period (*IP*)	0.8	103	104	104	106
Experimental conditions:					
1. Day of inoculation	+30	295	408	174	219
2. Inoculum density	0.001[2]	206	240	174	209

[1] Onset of tuber filling times 0.6, slope of allocation to tubers times 0.8.
[2] Inoculation postponed by 30 days.

growth during the early exponential phase (up to $LAI = 0.75$), which may increase yields considerably. Increasing *SLA*, which increases the light intercepting leaf area without reducing dry matter allocation to the tubers, has a less positive effect. Changing assimilate distribution such that tuber filling starts earlier, but at a slower rate, while leaf growth continues simultaneously for a longer period (as found in cv. Désirée; Spitters and Schapendonk, 1990), also increases yields, but only in blighted cultivars of the susceptible late type. Increasing the area of individual leaflets, which does not affect the total leaf area while allowing blight lesions to continue growth longer before reaching the edge of the leaf, hardly increases the epidemic rate and yield loss.

Tolerance to acceleration of leaf senescence. When acceleration of leaf senescence was neglected, yields of inoculated plots increased by 12 to 26% (Table 3). This corresponds to leaf senescence accounting for 4 to 15% of yield loss caused by blight in the experiments of 1987 and 1988. The remaining, major fraction of the yield loss thus was caused by direct leaf loss because of lesion extension.

Resistance components. The radial growth rate of lesions (*LG*) was the component that affected yield loss most (Table 3). The loss of green leaf area by coverage with lesions thus depended more strongly on the growth rate of existing lesions (determined solely by *LG*), than on the rate of formation of new lesions (determined in conjunction by *IE*, *LP*, *SI* and *IP*).

Experimental conditions. When inoculation was postponed thirty days, or inoculum density reduced by a factor of one thousand, the yield of late cultivars benefited most (Table 3).

Discussion

Yields in the 1988 experiment, where planting was delayed, were very low (Table 2). However, they were accurately modelled for all cultivars in both treatments, using the parameter values derived for 1987 except for the *LUE*. The successful simulations of host growth and epidemic development in the two years indicate that differences in yield loss due to *P. infestans* may be mainly explained by the incorporated differences between cultivars in partial resistance (*IE* and *LG*) and maturity class-dependent rates of leaf growth, leaf senescence and timing of tuber growth initiation.

The length of the growing season of control plants of late cultivars, such as Pimpernel, was overestimated by nearly a month for 1988 (Fig. 1D compared to 1B). This extra month of crop growth caused only a small overestimation of cumulative light interception and yield (Table 2) because of the low light intensity at the end of the season. In 1988, the crops were planted at June 1, while the relation between crop developmental stage and the temperature sum that was used in the model was determined for crops planted in April (Spitters and Schapendonk, 1990). The late planting may have caused foliage death at lower temperature sums than usual, especially for the control plants of late cultivars which reached into periods with much shortened daylengths and colder nights. Crop phenology of these cultivars may thus have been simulated poorly, causing the overestimation of the length of the growing season.

Growth and tuber yield of cv. Surprise were simulated well for both years and treatments, except for the unexplained overestimation of yield in the control treatment in 1987 (Table 2).

Earliness reduces yield loss (Table 2). Early cultivars escape part of the epidemics by completing a greater fraction of their tuber filling period before the disease causes premature foliage death. Therefore an altered assimilate distribution pattern, in which tubers are initiated earlier but leaf growth continues longer, simultaneously with tuber filling, increases the yield of blighted late cultivars (Table 3). When epidemics are initiated by lower levels of inoculum or at a later inoculation date, the yields of late cultivars also increase more than those of early cultivars (Table 3). Both intensity and timing of epidemics thus affect the differences in yield loss between late and early cultivars. Breeders should take this into account, when defining the required resistance levels of cultivars differing in maturity class.

The simulations show that late cultivars suffer more yield loss than early cultivars, when their levels of blight resistance are equal (Table 2). Experiments, on the other hand, often show a positive correlation between cultivar lateness and resistance (Umaerus et al., 1983). A possible explanation for this apparent contradiction may be that late cultivars have been subjected to a stronger selection pressure, in previous

resistance breeding work, precisely because of their low yields in the presence of blight. Another explanation may be that resistance has erroneously been equated to ground cover, which indeed is maintained longer by late cultivars (Figs. 1C, 1D). Ground cover or disease severity may only be useful as selection criteria for groups of genotypes of similar maturity class, but even then genotypes with uncommon patterns of assimilate distribution, such as cv. Désirée, may be wrongly assessed. Therefore measurement of resistance *components* is preferable (Parlevliet, 1979).

Acceleration of leaf senescence by the disease was shown to have caused 4 to 15% of the yield loss. However, no genetic variation for this aspect of tolerance has been found among the cultivars used (Van Oijen, 1991b). Photosynthesis and *LUE* are not affected by the disease in any of the three cultivars (Van Oijen, 1990, 1991a). Since, furthermore, other plant growth characteristics affect yield loss only slightly (Table 3), screening for increased levels of components of partial resistance is the best breeding strategy aiming at reduced yield loss due to late blight. If for the different resistance components similar levels of genetic variation are available, *LG* should be the main target of the breeding efforts.

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