Address by Keynote Speaker

Late blight: Its global status in 2002 and beyond

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The oomycete *Phytophthora infestans* (Mont.) de Bary, the causal organism of late blight of potatoes and tomatoes, continues to be the most important pathogen of potato crops throughout the world. The pathogen is feared by farmers worldwide because of its ability to destroy potato and tomato crops within a fortnight. It is thought that *P. infestans* originated and co-evolved on native wild tuber bearing *Solanum* species in the central highlands of Mexico (Reddick, 1939). The first documented experiences with late blight date from the period of 1842 to 1847, when devastating late blight epidemics swept through the potato growing area of North America and Europe, which was frequently commented upon in the daily papers.

Later, with the selection of less susceptible cultivars and the development of fungicides, the threat of the pathogen diminished. In the industrialized world, control of potato late blight is heavily dependent on fungicides. During the last decade despite frequent fungicide use, late blight epidemics have become more and more difficult to control (Turkensteen et al., 1997; Schepers, 2000). Crop losses due to late blight have been estimated to account for 10 to 15 percent of the total global annual potato production (CIP, 1996). Worldwide, the economic value of the crops lost, plus the costs of crop protection amount to 3 billion US $ annually (Duncan, 1999). It is evident that the problem with late blight is still not solved in a satisfactory way, neither in the industrialized nor in the developing countries. A key question is why late blight became and is still becoming more problematic.

The recent global resurgence of *P. infestans* is associated with the displacement of the old late blight worldwide spread population by a new, genetically more variable *P. infestans* population in many parts of the world (Spielman et al., 1991; Fry et al., 1993). These new populations include more aggressive genotypes of the pathogen (Day and Shattock, 1997; Flier et al., 1998; Flier and Turkensteen, 1999; Lambert and Currier, 1997, Turkensteen et al., 1997) and genetically variable populations (Drenth et al., 1994; Shattock et al., 1990; Spielman et al., 1991). In northwestern Europe, where both mating types are found, evidence is accumulating that sexual reproduction forms an integral part of the system (Drenth et al., 1994; Andersson et al., 1998) leading to populations of the pathogen with both sexual and asexual reproduction. There are also indications in the USA that field obtained isolates show characteristics that can be explained as their being sexual offspring of local clones (Goodwin et al., 1998). It appears that South America may soon follow (Adler et al., in preparation).

Sexual reproduction leads to genetic recombination, hence more variation, as well as the formation of oospores, which serve as a persistent source of soil-borne inoculum to bridge spells without green host plants. As observed in the field, oospore formation is the engine of genetic variation with a number of populations of *P. infestans*, and this variation can be in aggressiveness in infections of foliage (Figure 1, Flier and Turkensteen, 1999), of tubers, and of both foliage and tubers (Flier et al., 1998). Oospores are a major concern for the years to come, as the spread of 'new' blight strains and consequently sexually reproducing populations of *P. infestans* cannot be prevented. The present spread of oospore associated populations concerns Mexico and large parts of Western and Eastern Europe. Beyond 2002, *P. infestans* will continue to replace its single clone old population by more aggressive new population strains. Eventually, at all locations, asexually reproducing old and new populations will be replaced by both sexually and asexually reproducing populations. It is obvious that such events will have a considerable impact on epidemiology, host resistance expression, integrated late blight management, etc.

Pathways of primary field infections

The pathways to primary field infections are important aspects of both epidemic development and late blight control strategies. In the context of this article, a primary field infection is the first infection by a specific (sub)population of *P. infestans* from which an epidemic starts in a specified crop in a specified region. The primary field infection can be described specifically in regards to its origin or the genetic make up of the

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infecting spore. In regions, which are marked by climates with too cold, too dry or too hot spells for potato growing, there are two possible sources for initial inoculum to start epidemics: infected tubers and oospores.

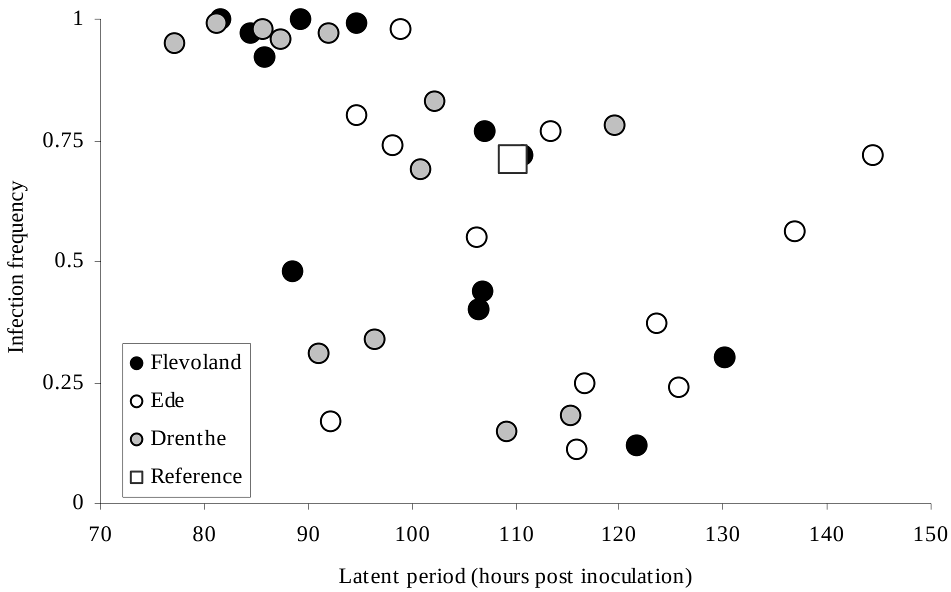

Figure 1. Variation in aggressiveness of isolates of *Phytophthora infestans* concerning infection frequency and latent period.

Infected tubers as a source for the next season inoculum is a well established and long known fact (Bonde and Schulz, 1943; De Bary, 1867; Löhnis, 1943; Melhus, 1915; Peterson, 1943). Tubers may become infected before harvesting, at harvesting or during storage (Dowley and Sullivan, 1991; Flier et al., 1998). Affected tubers may be disposed in waste piles or may end up as 'latently' infected seed tubers planted into the field. In the context of this article latently infected means that either tuber infection was externally not visible to the eye or unobserved.

The importance of potato dumps, as an important source of inoculum has been known for a long time (Bonde and Schulz, 1943; Van der Zaag, 1956). Potato plants develop on cull piles and dumps before, during and after planting time, until late blight kills them. They serve as first and massive sources of infection, giving rise to primary foci in the field. These inoculum sources are active long before others appear. As a consequence, when conditions are favorable to the spread of *P. infestans*, they overrule all other sources that appear later during the growing season. Control of such sources is a must for any potato grower. Through the Dutch farmers' organization LTO (Dutch Organization for Agriculture and Horticulture) a campaign called Masterplan Phytophthora has been initiated to control late blight. A primary goal was to neutralize late blight generated on cull piles. As a consequence of this campaign, the number of potato dumps was found to be effectively reduced during an inspection around mid April (Figure 2.; Masterplan Phytophthora, unpublished).

In the frame of the Masterplan Phytophthora, a study is being made on primary foci of *P. infestans* in the Netherlands to learn more about their impact and origin. A very striking type of primary foci started to show up around mid-June, 2000. Such foci were a central plant of which the mother tuber and all stems were affected. The subsoil (white) stem parts were apparently disease free, whereas around the nodes, lesions developed at all levels. The plant development and vigour did not appear to differ from healthy neighbor plants, but the neighboring plants had mainly foliar lesions. Of the primary foci studied in 2000, 13 out of 27 were a central plant with a diseased mother tuber (Table 1). Over the period 2000– 2001, more than 50% of the primary foci studied were of this type. It is assumed that these diseased mother tubers originated from latently infected seed. However, the symptoms of a diseased mother tuber linked with diseased stems, as described above, do not agree with past descriptions of primary foci developing from diseased seed tubers (Van der Zaag, 1956; Murphy and MC Kay, 1927; Wallin and Polhemus, 1956) where plants emerged from less than two percent of the diseased tubers (Boyd, 1980; Hirst and Stedmann, 1960) and, in most cases, these plants had a single weak stem that was totally diseased.

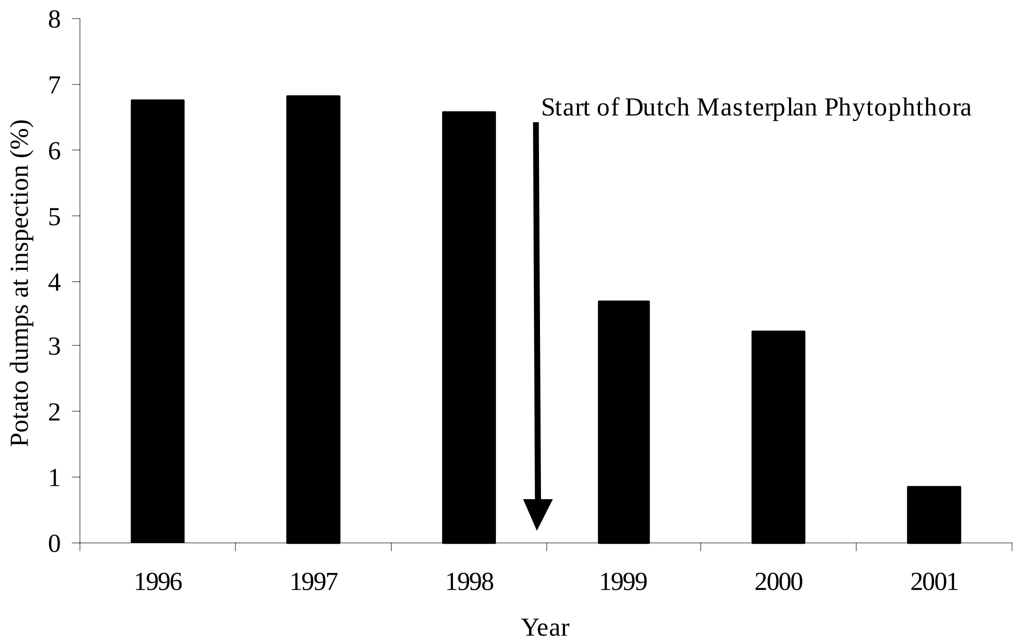

Figure 2. Effect of the Masterplan Phytophthora on the decrease in the numbers of waste dumps in the Netherlands during 1996 – 2001.

Table 1. Sources of early outbreaks of *Phytophthora infestans* in three different potato-growing areas in the Netherlands, June 2000.

	Source				
Region	Infected mother tuber	Dump	Distant source	Volunteer potatoes	Unknown (including. oospores)
Northeast (Starch potato area)	8	2	0	0	0
Southeast (Ware potatoes)	2	0	5	2	1
Southwest (Seed and ware potatoes)	3	0	4	0	0
Total	13	2	9	2	1

The discovery of diseased plants arising from diseased seed tubers rather late after emergence is in agreement with results of research on latently infected seed tubers in Germany (Adler, 2001; Habermeyer and Adler, 2000). Using a PCR-technique they demonstrated that symptom free tubers in storage were latently infected. Such latently infected tubers developed symptom free sprouts, which were found to be latently infected based on the PCR-test. In the field, plants developing from such tubers initially appeared healthy, but developed massive stem lesions when they approached full growth.

Seed, as a source of primary inoculum, has been proposed by many authors (Bonde and Schulz, 1943; De Bary, 1867; Löhnis, 1943; Melhus, 1915; Peterson, 1943) to be the main vehicle for the old population of *P. infestans* to get from a prior crop to the next one. Nevertheless, in the past, few early field infections were found to be linked with diseased seed tubers (Van der Zaag, 1956). As nobody was aware of the relatively late occurrence of primary diseased plants from latently infected seed tubers, such infections were not observed at the proper time in a proper way and thus, have been overlooked.

Nevertheless, with respect to latently infected tubers, there are other consequences. The refrigerated storage facilities available to an ever-growing number of countries contribute to the amount of latently infected (seed) tubers. In addition, these latently infected tubers are ideal for long-range dispersal of *P. infestans*, and hence contribute to the globalization of the new population of late blight strains. It is remarkable that more than 150 years after the introduction of late blight into the USA and Europe we are still learning basic elements of the epidemiology of *P. infestans* and, especially, how epidemics start in the field.

Rapid epidemic development of late blight urges for an early preventative approach as the first line of defence. Identification and eradication of initial inoculum sources (on a national or regional scale) is an important feature, of which awareness of farmers and extension workers should be improved. This concerns such matters as optimizing the timing of the first fungicide application to high-risk seed lots and potato fields, and the incorporation of risk assessment of inoculum sources in integrated blight management programs.

Volunteer plants are very common in vast parts of Europe. Volunteer potatoes are associated with mild winters during the last decade in northwestern Europe. Volunteer plants have a very strong impact on epidemics. They are implicated in the generation of uncontrolled epidemics that are marked by a massive buildup of inoculum. In addition, because multitudes of oospores have been found on volunteer plants, they also contribute to generating and maintaining genetic variation, as well as providing a persistent source of soil borne inoculum. However, volunteer plants did not appear to be a major source for the earliest primary foci in field crops during most years of the survey done in the framework of the Masterplan Phytophthora. In the Netherlands, hibernation of *P. infestans* in volunteer tubers in the field appears to be a rare event (Zwankhuizen et al., 1998). In relatively few occasions early primary foci of volunteer potatoes were found that appeared to be associated with oospore based infections. However, this spring (2002) many primary foci were found in 'volunteer plants' of last year's non-harvested crops and most likely, those foci are oospore related.

Oospores appear to be effective as a source of primary infections (Drenth et al., 1995; Andersson et al., 1998; Turkensteen et al., 2000). Oospores may germinate at any time during, before and after the growing season. However in most years, oospore generated infections appear not to be a source of primary infections in very young crops (Andersson et al., 1998). Apparently, very wet field conditions are needed for the generation of oospore based infections. Infections thought to be caused by oospores were found associated with flooding of the fields for 24 hours or more by precipitation. In spring 2002 such conditions occurred around the end of April in the Netherlands. In those fields where volunteer potatoes had emerged before that period and where they were still present around mid-May and later, there were many small foci of *P. infestans* found in such fields only, which can only be explained by oospore generated infections.

Pathways to chemical control of late blight

Concerning control of late blight by chemical products, two aspects are of importance. It concerns the so called 'window of effective operation' and the farmers' game called 'Russian Roulette'.

The window of effective control concerns a span of time and refers to the number of days during which the crop is adequately protected by a fungicide. It depends on the growth stage of the crop, characteristics of the fungicidal compounds, weather conditions, host resistance, infection pressure and aggressiveness of pathogen strain concerned. The present day short disease cycles of sometimes less than 2.5 days demand a vigilant attitude by farmers. Nevertheless, the majority of farmers still prefer to spray according to the calendar. However, spraying every 4 days can be quite risky with the potential of 2.5 day disease cycles in the field.

The concept of the farmers' game Russian Roulette is based on the following rules. Not all critical periods occur during the periods of poor protection. Critical periods during low protection periods do not always lead to infection of the crop, which is especially the case at the beginning of the growing season when infection pressure is still low. By sheer luck, the majority of the farmers, which apply calendar spraying, escape with minor or no damage. The group of escapee's truly believes that they did all well and tell that loudly to everyone. At conferences on the risk of spraying with too long intervals these persons are a pain in the neck for the lecturer. On the other hand, the group of victims truly believes they made a mistake somewhere with blight control and keeps that to themselves. Russian Roulette has a similar outcome; a very talkative group and a strikingly silent one. Instead of applying calendar spraying, it is strongly recommended to spray according to a decision support system and to keep a careful record on the dates and times of spraying in relation to forecasted and recorded risk periods and thus fine-tuning the control strategy against the late blight pathogen.

Pathways to resistance of the host

Resistance is an important cornerstone of integrated late blight management. To counterbalance the increased level of aggressiveness of the 'new' blight, a considerable level of host resistance is required in present and future potato cultivars. There is confusion on the fate of host resistance regarding its stability, durability and levels of resistance expressed in the field as compared to values for resistance presented in variety lists. In the past late blight resistance breeding was solely directed to resistance against the US-1 clonal lineage that was distributed worldwide, and thus based on the virulence of a slowly evolving single clone population of the pathogen. Resistance was simply subdivided into durable or field resistance and non-durable or R-gene based resistance. With the introduction of more genetic variability and more aggressive strains of the pathogen, general resistance levels were observed to be considerably lower than before (Figure 3). In the turbulent interaction with 'new' population strains, resistances which were considered as exemplary for durable resistance show race-specificity, thus suggesting that the action of R-genes for foliar and for tuber resistance were independent from each other (Flier et all, 2001; Peters et al., 1999; Platt and Tai, 1998). A typical example is cultivar Pimpernel. Possessing a resistance mechanism dependent to day length, cv. Pimpernel was used as an important standard for high levels of foliar blight resistance under long day conditions. It was also regarded as the high-level resistance standard variety for tuber blight resistance. At present it shows that same level of resistance with some isolates and with others it reacts as extremely susceptible (Flier et al., 2001). Experiences gained in the past on resistance appear to be less valid at present. In fact, prospecting for host resistances is an important feature for the near future (Inglis et al. 1997). Promising sources of resistance are present in species like *Solanum demissum* and related species (Toxopeus, 1964) and *S. bulbocastanum* (Hermsen and Ramanna, 1973).

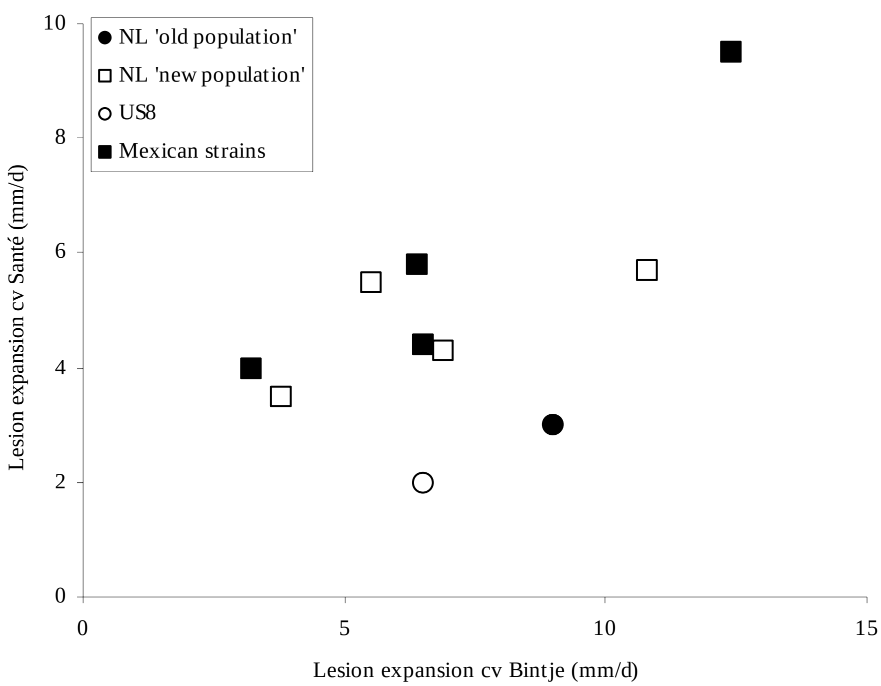

Figure 3. Variation in lesion expansion of *Phytophthora infestans* isolates representative for four different populations of the pathogen measured on a susceptible (Bintje) and partially resistant (Santé) potato cultivar.

How to address the tester strain issue? How to cope with the more complex blight situation in breeding programs? A principal problem with breeding for resistance to late blight is the isolate (strain, race) used for resistance testing. Such a strain should be representative for the population of *P. infestans* in 12 to 20 years from now. It is questionable whether testing can ever be performed again with a single isolate compatible to all sources of resistance available. A first approach is to collect isolates found to attack resistant progenitors, breeding lines and advanced materials at regions of origin and at the locations of their introduction. Constant monitoring of *P. infestans* population structure is needed to keep record of changes of populations of *P.*

infestans regarding resistances in order to adapt and update resistance-screening protocols. For this purpose an adequate database should be set up and maintained, as well as a collection of isolates for breeding and testing purposes.

R-gene or R-gene free, that is the question. There is some animosity between the groups which advocate R-gene free breeding and the groups which believe in deliberate R-gene (accumulation) breeding.The fate of R-genes is that sooner or later they will loose effectiveness because of compatible strains showing up. However, it is wise to ask whether a breeder can actually choose to go for R-gene-free breeding. The following are three basic rules on resistance to late blight:

- Rule 1. R-genes may contribute to partial durable resistance through linkage and/or pleiotropic effects.
- Rule 2. There is solid evidence that R-gene breeding can yield very susceptible cultivars, which has been i.e. the case with cultivar Vertifolia, which possessed four R-genes (R1,R2,R3,R4) (Van der Planck 1971; Turkensteen, 1993).
- Rule 3. There is solid evidence that good levels of resistance can be obtained after removal of R-genes from breeding populations (Turkensteen, 1993).

All three basic rules appear to be true, but they cannot all be true at the same time in the same clone or same resistance background. Nonetheless, breeders can apply the rules in the most profitable way according to their specific situation.

Some inferences from the basic rules: As Rule 2 is always valid, testing is needed for the presence of both R-genes and the level of other resistances during the crossing stages of the breeding program. Hence, expertise, good laboratory facilities and capital are required. Where deliberate breeding for R-gene (accumulation) is possible, do so if feasible. However, in the case that specific late blight expertise, testing facilities or money is not available, such an approach is eithert not possible or very risky and therefore not advisable. R-gene-free breeding is not a dogma, but just a pragmatic approach to prevent hitch hiking of R-gene based, non-stable forms of resistance in cases where facilities, money and expertise are not available to do proper testing.

Pathways beyond 2002

Resistance breeding with existing and novel sources of resistance should have a high priority to counterbalance increased aggressiveness of the new populations of *P. infestans*. In fact, higher levels of resistance are the only way to compensate for the impact of oospore based epidemics and the more rapid epidemic development of the pathogen. Therefore, prospecting all known sources of resistance of the host and matching virulence and aggressiveness of the pathogen is a primary necessity.

All bits and pieces of useful knowledge are to be integrated to develop more effective integrated control strategies. The combined use of host resistance, disease forecasting and effective fungicides will have a decisive impact on the improvement of integrated blight management. Basic knowledge on the processes and genes involved in: host resistance, pathogenicity and aggressiveness is still fragmentary and should be acquired as soon as possible. Efforts on basic and applied research on these aspects should be strengthened.

Constant monitoring of *P. infestans* populations in relation to epidemic parameters and stability of resistance is a very important issue. GILB should take the responsibility to coordinate such efforts on an international scale. Construction of robust integrated blight management strategies including decision support tools to improve blight control worldwide appears to be the proper response to the new situation with the late blight pathogen. However, for this purpose a better understanding of evolution and speciation in (host specific) late blight populations in relation to adaptation to host resistance are a most important aspect of this all-over approach

With the ongoing spread of sexually reproducing populations, the less developed countries are going to suffer the most. It should be brought to the awareness of policy makers that for many traditionally potato growing regions disaster is eminent. The scientific expertise and authority united under the umbrella of GILB makes this organization a powerful platform to address politicians and policymakers on the development with late blight and to advise them how to respond on the short and mid long term. GILB should serve as a very important forum for addressing this threat for potato production beyond 2002

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