REVIEW ARTICLE

Late blight of potato: From the great Irish potato famine to the genomic era – An overview

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Summary Late blight of potato and tomato, one of the most widely reported diseases of plants, is a significant curb in global agriculture which poses severe problems in terms of yield and economic losses, and environmental pollution due to pesticides use. The disease is caused by *Phytophthora infestans* -an oomycete - which first drew the considerable attention of plant pathologists during the mid-1840s when the pathogen incited historic starvation in Ireland – the great Irish potato famine - as a consequence of substantial potato losses due to late blight disease. Since that period, late blight has triggered several epidemics of potato and tomato of profound intensity in different regions. Over the course, synthetic fungicides have been proved effective management practice for late blight control; nonetheless, the evolution of new genotypes with increased virulence to hosts and resistance to fungicides has been greatly regarded as an agricultural problem. Breakthroughs in genome sequencing of *P. infestans* and identification of resistance genes in some plants have opened ways for the development of resistant genotypes. However, there still exist numerous challenges to deal with this noxious pathogen. This review aims to highlight the historical significance of late blight disease, its chemical control strategies and associated challenges, and resistance breeding programs by employing genetic approaches.

Additional Keywords: Breeding, pesticides sensitivity, qualitative and quantitative resistance, resistance genes, virulence

Introduction

Late blight of potato, induced by an oomycete pathogen, *Phytophthora infestans*, is a significant curb in global potato production which has severe effects on the crop, yield, and quality of tubers. The disease has been an important limiting factor for potato production worldwide and a major contributing element in financial losses in terms of fungicide application (Hijmans *et al.*, 2000). Outcomes of late blight are propounded in temperate and moist regions which facilitate *P. infestans* and proliferation of the disease

with hastened intensity (Nowicki *et al.*, 2012). The disease first appeared in the US during 1842-43 (Peterson *et al.*, 1992). However, devastating effects were observed in Ireland during 1845 when the pathogen wiped out potato crop throughout the country triggering famine – the Great Irish famine- which is believed to have caused the death of more than two million Irish population (O’Grada, 1999; Scholthof, 2007).

Due to the popularity and importance of potato – the third most cultivated crop following rice and wheat – understanding and controlling the limiting factors which have profound impacts on potato yield are crucial for avoiding future food issues. Advances in synthetic chemistry have greatly contributed to minimal losses of potato by the development of fungicide compounds which have shown good efficiency in controlling the disease epidemic throughout the world for almost a century. However, the

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use of such fungicides is of grave concern because they may cause environmental issues and increased resistance of *P. infestans* strains to oomycetocides (Qin *et al.*, 2016; Majeed *et al.*, 2017a; Zhang *et al.*, 2017).

To address environmental challenges posed by fungicide application and the emerging strains of the pathogen which are less responsive to some of the fungicides, research activities during the last few years have been diverted to find out alternative substances of natural origin, biocontrol agents (BCAs), and introgression of resistance genes of interest in the hosts from some wild sources, which could efficiently reduce high reliance on fungicides in future (Daayf *et al.*, 2003; Dorn *et al.*, 2007; Śliwka *et al.*, 2014). Several efforts have been made in this regard to introduce natural formulations and BCAs as alternative sources of fungicides and breeding for resistance development in host crops (Lenman *et al.*, 2016; Ippólito *et al.*, 2017; Roman *et al.*, 2017; O'Brien, 2017; Tala *et al.*, 2018). However, identification, isolation, preservation, and consistency in the effectiveness of natural compounds and BCAs in laboratory and field remain great challenges for researchers (Velivelli *et al.*, 2014). Moreover, qualitative resistance breeding approaches in cultivated potatoes have been proven less effective due to the potential of *P. infestans* to overcome such single gene-controlled resistance (Rietman *et al.*, 2012). On the other hand, the search for quantitative resistance and introgression of multiple resistance genes in potatoes against the pathogen seems a promising quest to endure late blight resistance (Rietman *et al.*, 2012; Sarkar, 2015). Although we have not been able to develop a durable resistant potato cultivar, nor have formulated an efficient biocontrol agent alternative to fungicides, still there exists a great hope for sustainable management of late blight of potato through further expansion in the genomic understanding of the host and pathogen interaction. This review aims to highlight historical perspectives of late blight, its chemical control and challenges, and resistance breeding in the genomic era.

Late blight in history

There is sufficient documentary evidence that late blight (LB) had occurred in some parts of the United States during 1842-43 (Peterson *et al.*, 1992; Andrivon, 1996; Tateosian *et al.*, 2017), reaching to Canada, Belgium, Holland, Italy, Germany, Scotland, and the UK during 1844 and 1845. However, first profound effects of the disease appeared by the mid of 1845 in Ireland where it caused a devastating catastrophe which triggered food starvation and consequent Great Irish Famine (Ristaino, 2002; Scholthof, 2007). It is believed that the famine resulted in a population drop in Ireland from 8.2 to 5.5 million due to human deaths and migrations (Cantwell, 2017). At the time of famine and years later, the exact causal agent of the disease was cynical and different views were expressed about the calamity of the famine arbitrating towards environmental conditions and a fungus called *Botrytis infestans*. It was de Bary in 1870 who first described the causal agent as *P. infestans* and opened ways for further research and subsequent formulations of antimicrobial compounds (Turner, 2005). In succeeding years after the famine, late blight disease remained major havoc in most parts of the world until the introduction of the Bordeaux mixture in the late 1880s which significantly contributed to the management of blight incited crop damages (Haverkort *et al.*, 2008). For instance, due to rare chemical control approaches in Finland, the disease had major epidemics in the country until the 1970s (Hannukala *et al.*, 2007). During 1916-17, substantial potato losses occurred in Germany due to poor management of late blight disease as a result of a shortage of Bordeaux mixture which led to famine - generally attributed to causing several deaths of the German soldiers (Mizubuti and Fry, 2006). Outbreaks of late blight occurred with severe intensity in different parts of the USA particularly Oregon and Washington during 1947, 1974, and 1990s (Johnson *et al.*, 1998) and the USA and Canada during 1980-1990 which resulted in considerable losses of both po-

tato and tomato (Fry and Goodwin, 1997). In 2009, the USA experienced another episode of late blight causing significant crop damage to tomatoes (Fry *et al.*, 2013). In the Netherlands, a comprehensive analysis of data covering the period between 1950 and 1996 revealed the different intensity of late blight disease in the region (Zwankhuizen and Zado, 2002). In northern and southern parts of India, Oman, Tunisia, Nigeria, China, and Chile considerable losses for potato and tomato growers were incurred by *P. infestans* during a different period of times from 1953 to 2012 (Chowdappa *et al.*, 2015; Fry *et al.*, 2015). The occurrence of late blight and its devastations are not limited to the aforementioned regions; rather it has recurrently appeared in different parts throughout the world with a differential intensity of damages depending on the climatic conditions, the potato varieties, and growers' approaches to manage the disease in those regions. The disease remains a challenging problem for agriculturalists throughout the world in climates suitable for the spread and establishment of the pathogen (Majeed *et al.*, 2017a).

Phytophthora infestans is generally believed to have its origin in Mexico from where the pathogen migrated to several parts of the world (Andrison, 1996). The migrations are thought to have occurred either from Mexico to the USA and subsequently to Europe or from Andean regions to the USA and Europe or probably from Mexico to Peru, USA, and then to Europe with the further general perception that the disease could have spread to several other parts of the world through those migrations after the 1850s when potato production had been established in the world (Andrison, 1996; Mizubuti and Fry, 2006).

An important factor linked with emerging threats of the late blight pathogen is its changing population structure globally. Frequent studies suggest that before the 1980s, the global population of late blight pathogen consisted of a single clonal lineage (A1) which reproduced asexually, while in Mexico both lineages (A1 and A2) co-occurred

with the tendency of asexual and sexual reproduction (Andrison, 1996; Mizubuti and Fry, 2006; Runno-Paurson *et al.*, 2014). Probable migration of A2 mating strains of *P. infestans* from Mexico to Europe during 1976 could have resulted in sexual reproduction, the formation of oospores, diversity in population structure, the virulence of the newly introduced strains, and difficulties in disease control methods (Hannukkala *et al.*, 2007; Runno-Paurson *et al.*, 2014). The dominant method of reproduction of *P. infestans* is asexual where sporangia and zoospores are produced. Sexual reproduction occurs following the mating of the compatible strains and results in the formation of oospores which are resistant to unfavorable environmental conditions (Nowicki *et al.*, 2012; Lehsten *et al.*, 2017; Rekad *et al.*, 2017).

Evolution of fungicides and emerging challenges

Until the 1880s, potato late blight appeared to be a challenging threat to potato growers throughout the world because there was no curative treatment to control the disease. The first-ever fungicide, the Bordeaux mixture (a mixture of lime and copper sulfate) when formulated in the mid-1880s, opened ways for the efficient control of late blight and several other plant pathogens (Ayres, 2004; Lemire *et al.*, 2013). Since the development of copper fungicides, late blight was successfully managed by the exhaustive application of these compounds. After the 1950s, several other fungicides containing different chemical ingredients and diverse modes of actions were progressively developed which further strengthened the disease control methods and contributed to greater yields of potato crop (Haverkort *et al.*, 2008). However, successive use of newly developed fungicides, particularly metalaxyl compounds, appeared gradually less effective in controlling the disease during the 1980s as a result of selection pressure and resistance induction in population of *P. infestans* in several parts of the world (Cooke

et al., 2011; Haesaert *et al.*, 2015). Reports about the insensitivity of *P. infestans* strains to commonly used fungicides from the USA, Europe, Asia, Middle East and the rest of the world were documented in the 1980s (Goodwin *et al.*, 1996; Cooke *et al.*, 2011; Fry *et al.*, 2015). The resistance development to fungicides in isolates of *P. infestans* is yet to be fully explored, however, studies suggest that mutation, sexual recombination, the role of semi-dormant locus, the influence of quantitative trait (controlled by major and minor genes), and changes in ribosomal RNA could greatly contribute to the insensitivity of the new strains of the pathogen to fungicides (Lee *et al.*, 1999; Randall *et al.*, 2014; Fry *et al.*, 2015; Qin *et al.*, 2016).

Besides stimulation of fungicidal resistance, the use of fungicides for late blight control has drastic implications on the environment, ecosystem, and human economy. Under environmental conditions favorable for the disease spread, cultivation of susceptible cultivars may substantially increase the input of synthetic chemicals into the agricultural fields. For instance, in Netherlands, Belgium, and other countries where wet and cool climate prevails during potato growth, the spray frequencies of oomycetocides may exceed 20 applications per growing season (Haesaert *et al.*, 2015). Estimated economic costs mainly incurred by fungicide application in the USA are reported to be 0.287 billion dollars, in Netherlands and Belgium 68-124 billion while such estimates exceed 6.7 billion dollars globally on annual basis (Haverkort *et al.*, 2008; Haesaert *et al.*, 2015; Liu *et al.*, 2016). These estimates are generally variable because climatic conditions in different countries vary significantly and there is no proper monitoring system to collect exact data regarding actual costs and damages to potato crops due to late blight disease and the volumes of used fungicides. The first use of copper-related fungicides raises issues of risks for environmental pollution and ecosystem stability and these risks have even arisen over time with the development of more sophisticated compounds (Aktar *et al.*, 2009).

Resistance induction: successes and challenges

In the context of sustainable use of pesticides for the control of late blight, forecasting systems and integrated disease control measures can work in reducing the use of fungicide applications and their input (Cooke *et al.*, 2011; Majeed *et al.*, 2017b). Seemingly, one of the most efficient quests for late blight control is to develop resistance in potato crop to the pathogen. For durable resistance induction, identification of genes and loci with potential resistance-conferring abilities is the key step in breeding for resistance efforts. However, such a goal may not be easy to accomplish because of the evolution of pathogens to overcome such resistance with time and thus, more systematic approaches are consistently required which may employ wild sources for discovering resistance genes (Nelson *et al.*, 2018).

Efforts have been made through decades by employing conventional and molecular breeding approaches for induction of the required resistance in potatoes against *P. infestans*. Genome sequencing of *P. infestans* (Haas *et al.*, 2009; Martin *et al.*, 2013) and potato (Xu *et al.*, 2011) has fostered a wide scientific interest in looking for several durable disease resistance strategies, i.e., manipulating crosses between susceptible and resistant *Solanum* species, introgression of genes from resistant donors, understanding the pathogen and host proteins involved in host-pathogen interaction, using biotechnological approaches to enhance the immunity of potato against *P. infestans*.

To date, many blight-resistant genes (BRG) from wild species and hybrids of *Solanum* such as *S. demissum* (*R1-R11*), *S. bulbocastanum* (*Rpi-blb1-Rpi-blb3*), *S. stoloniferum* (*Rpi-pta* and *Rpi-sto1*; *Rpi-sto2*), *S. michoacanum* (*Rpi-mch1*), *S. americanum* (*Rpi-amr3*), *S. ruiz-ceballosii* (*Rpi-rzc1*) and several others have been identified and successfully mapped into different chromosomes of cultivated potato (Sliwka *et al.*, 2006; Bradshaw *et al.*, 2006; Hein *et al.*, 2009; Sliwka *et al.*, 2012a,b; Du and Vleeshouwers, 2017; Agu-

ilera-Galvez *et al.*, 2018). The introduced *R* genes particularly R1-R11 in domestic potato proved effective against *P. infestans* for long period until the evolution of new strains of the pathogen which have overcome those *R*-genes, thus making qualitative resistance a non-durable approach (Sliwka *et al.*, 2006; Vleeshouwers *et al.*, 2011; Du *et al.*, 2017). Qualitative resistance which relies on major *R*-genes offers wide-ranging resistance against the pathogen by the production of proteins in host tissues which recognize the pathogen; defeating of major *R*-genes by the newly evolved strains of *P. infestans* however, suggests quantitative disease resistance conferred by many genes (often termed as minor genes) framed into quantitative trait loci as a better strategy, although difficult to be accomplished (Du *et al.*, 2015; Nelson *et al.*, 2018).

Since resistance based on single *R*-genes corresponds to hypersensitive response in a host but such durability is not persistent, there is a strong need for isolation and employment of more *R*-genes in pyramids (Aguilera-Galvez *et al.*, 2018). A large number of wild species of *Solanum* with efficient resistance to *P. infestans* have been described which may serve as valuable donors of *R*-genes however major challenges emerge when it comes to cross them with a cultivated potato because of variation in ploidy level (Smyda *et al.*, 2013). Quantitative resistance conferred by minor genes may either be deployed in potato after successful identification and isolation or the potato may itself harbor such type of resistance. However, those minor genes may interfere with major *R*-genes, influencing the quantitative resistance ability of the host, thus posing another challenge to durable resistance quests (Ewing *et al.*, 2000). Further, dependence only on *R*-genes, focus on other plant genes which encode defense-responses and pattern recognition immune receptors in the host can work better in achieving durable late blight resistance (Du and Vleeshouwers, 2017). Moreover, staking numerous *R*-genes and quantitative trait loci in a single genome can enhance the resistance

potential of the host to the pathogen (Nelson *et al.*, 2018).

In addition to *R*-genes searches, effectoromics, transcriptomics, metabolomics and cis-genic approaches may greatly foster our knowledge about resistance induction in potatoes against the pathogen. Recently Gromadka *et al.* (2018) described that calcium-dependent protein kinases had a strong relation with host-defense against *P. infestans*, whose elevation in potato seems an ideal approach to suppress pathogenic stress. Domazakis *et al.* (2017) argued that effectoromics could potentially boost our efforts for blight-resistance development because the employment of such techniques assists in the identification of pathogen-recognition receptors. Aguilera-Galvez *et al.* (2018) believed that effectoromics screening of the interaction between avirulence (*Avr*) and *R*-genes in *Phytophthora-Solanum* pathosystem could lead to broad-spectrum late blight resistance in potato. Haverkort *et al.* (2016) proved that cis-genic introgression of *R*-genes into potato clones exhibited a high degree of late blight resistance in field trials.

In conclusion, late blight, one of the costliest plant diseases, is generally managed by the widespread application of fungicides. Environmental, ecological and health risks associated with fungicide application have resulted in an increased search for sustainable disease management. Induction of resistance against *P. infestans* in cultivated potato from wild sources has been long practiced; however, introgression of *R*-genes which confer only race-specific resistance has been overcome by new races of the pathogen. Therefore, quantitative resistance by employing many genes could offer durable resistance. Moreover, search for genes associated with host immunity other than *R*-genes can boost disease resistance approaches. Although there are several challenges in the accomplishment of late blight resistance programs, a comprehensive understanding of the pathogen and its host genome has the spacious potential for further improvement in resistance breed-

ing. Identification, isolation, and pyramiding of new sources of genes with durable resistance to *P. infestans* into potato would be possible in near future with the help of effectoromics, transcriptomics, metabolomics, and cis-genic approaches.

List of abbreviations:

(Avr): avirulence

BCAs: Biocontrol agents

BRG: Blight resistance genes

LB: late blight

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ΑΡΘΡΟ ΑΝΑΣΚΟΠΗΣΗΣ

Περονόσπορος της πατάτας: Από τον Ιρλανδικό λιμό της πατάτας στη γονιδιωματική εποχή - Μια ανασκόπηση

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Περίληψη Ο περονόσπορος της πατάτας και της τομάτας, μια από τις πλέον ευρέως διαδομένες ασθένειες των φυτών, αποτελεί σημαντικό περιορισμό στη γεωργία παγκοσμίως προκαλώντας σοβαρά προβλήματα στην παραγωγή με οικονομικές απώλειες και επιβάρυνση του περιβάλλοντος με τη χρήση φυτοφαρμάκων. Η ασθένεια οφείλεται στον ωομύκητα *Phytophthora infestans*, ο οποίος τράβηξε για πρώτη φορά την προσοχή των φυτοπαθολόγων στα μέσα της δεκαετίας του 1840, όταν προκάλεσε τον ιστορικό λιμό στην Ιρλανδία -τον μεγάλο Ιρλανδικό λιμό της πατάτας- ως αποτέλεσμα των σημαντικών απωλειών στην παραγωγή πατάτας από την ασθένεια. Έκτοτε, ο περονόσπορος έχει πυροδοτήσει αρκετές επιδημίες μεγάλης έντασης στις καλλιέργειες πατάτας και τομάτας σε διάφορες περιοχές. Με την πάροδο του χρόνου, τα συνθετικά μυκητοκτόνα έχουν αποδειχτεί αποτελεσματική πρακτική για την αντιμετώπιση του περονόσπορου. Εντούτοις, η εμφάνιση νέων γονοτύπων με αυξημένη παθογόνο δύναμη και αντοχή στα μυκητοκτόνα θεωρείται σε μεγάλο βαθμό ως πρόβλημα στη γεωργία. Σημαντικές ανακαλύψεις στην αλληλουχία του γονιδιώματος του *P. infestans* και ο προσδιορισμός γονιδίων ανθεκτικότητας σε ορισμένα φυτά έχουν ανοίξει δρόμους για τη δημιουργία ανθεκτικών γονοτύπων. Εντούτοις, πολλές προκλήσεις εξακολουθούν να υφίστανται αναφορικά με το συγκεκριμένο επιβλαβές παθογόνο. Η παρούσα ανασκόπηση έχει στόχο να υπογραμμίσει την ιστορική σημασία του περονόσπορου, τις στρατηγικές χημικής αντιμετώπισής του και τις σχετικές προκλήσεις, και τα προγράμματα δημιουργίας ανθεκτικών γονοτύπων χρησιμοποιώντας γενετικές προσεγγίσεις.

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