
REVIEW

Current perspectives on the population structure of *Phytophthora infestans* in India and their relation to the management of late blight disease of potato

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Phytophthora infestans, the casual organism of late blight of potatoes and also tomatoes is an iconic and extremely well-known plant pathogen responsible for the formal inception of the study of the discipline of plant pathology and hence needs little introduction. Globally, late blight disease can add up to 3–10 billion USD loss annually. India, the 2nd largest producer of potatoes worldwide, has approximately Rs. 2600 crores in yield loss and management costs per annum. Despite tremendous developments of discovering several resistance (R) genes in wild Solanaceous relatives, avirulence RXLR effector proteins and their co-evolution, genome organisation, and their application in agriculture, *Phytophthora infestans* continues to threaten potato and tomato production worldwide, necessitating the use of expensive fungicides for management. The sudden disruptions due to the epidemic also have socioeconomic consequences for the resource-poor farmers. Modern management methods therefore take into consideration the phenotypic and genotypic diversity of the lineages, which is largely clonal through asexual reproduction as evidenced in India, or rarely sexual elsewhere. The different clonal lineages determined through a standard set of 12-plexed SSR markers have shown different sensitivity to fungicides, etc. These clonal lineages have been detected through continuous surveillance and successfully incorporated into late blight management strategies in the UK (via the EuroBlight) and the USA (via the USABlight). Similar surveillance in India by the author's laboratory has shown that currently, all Indian late blight populations are of the European 13_A2 clonal lineage with 115 sub-clonal lineages, of which 90 are unique to the country across the potato-growing regions and have additional diversity of host and temperature-adapted clonal lineages, showing increasing insensitivity to commercial late blight targeted fungicide formulations, like mancozeb, dimethomorph, etc., thereby making it even more necessary to implement this strategy. In India, a regional pathogen population structure was observed with evidence for local migration, cross-border movement between surrounding countries, and introductions via imports. There was also evidence of genetic drift and between-season transmission of more strongly pathogenic subclones with a complete displacement of some sub-clonal types each year. However, it is essential to understand that these attributes are dynamic in time and therefore continuous surveillance of LB populations is necessary for effective disease management. Surveillance networks for LB like the Euroblight (for Europe), and USA Blight (for USA), for crop protection and the prevention of epidemics, is also there for Asia, i.e. AsiaBlight, with 15 member countries in which India is a member. A paradigm policy change is urgently needed in India to incorporate the diversity of the population structure of *Phytophthora infestans* into disease management strategies for effective late blight disease management.

Keywords : Late blight of potato, *Phytophthora infestans*, crop protection, R genes

Phytophthora infestans, the casual organism of Late blight of Potato and Tomato needs little introduction to mycologists and plant pathologists as all undergraduate textbooks on plant pathology and mycology compulsorily include this pathogen explaining how before the advent of Louis Pasteur's germ theory of disease (Lindley, 1845),

when the cause of diseases could be anything as varied from a curse from God, bad weather, the laziness of the Irish, or a minute fungus (Berkeley, 1846 (1948); Lindley 1845; Bourke 1993); a casual organism was first correlated with disease and in this case, identified in 1846 by M. J. and subsequently renamed *Phytophthora infestans* in 1876 by Anton de Bary (Berkeley, 1846 (1948); De Bary, 1876; Bourke 1993) leading to the systematic start of the discipline of Plant pathology. The Irish Potato Famine (Woodham-

Smith, 1962) caused by this disease that plagued Ireland for 7 years (1845–1852) leading to mass starvation of the Irish people and emigration of half of the population; considering its social relevance has moved beyond the realm of plant pathology and mycology textbooks to social science and literature. Irish Famine memorials can now be found in at least 15 places worldwide (Australia, Britain, Canada, Ireland, Northern Ireland, United States) spread across various continents. Technically though, the disease first occurred in the United States in 1843 around the ports of Philadelphia and New York (Stevens, 1933; Bourke, 1964) from where the plant disease pandemic spread over three years to more states and provinces in the northeast US and Canada and by 1845 was reported in Europe, the UK and Ireland. Potato late blight again became a major influence in human affairs in the closing year of World War I, when the 1918 epidemic was among the forces that led to Germany's surrender (Miller and O'Brien 1955). In contemporary times, 1200 million people could be fed by lost food due to this disease (Fisher *et al.* 2012) and globally late blight disease can add up to 3–10 billion USD per annum in yield loss and management costs. (Haverkort *et al.* 2009; Kamoun *et al.* 2015).

In the Indian context, the country is the second largest potato producer worldwide and is the 3rd principal crop after rice and wheat. In the past twelve years, India has experienced at least three severe late blight epidemics (2009, 2014 and 2019) in different parts of the country (Guha Roy *et al.* 2021), and this is the greatest limiting factor towards potato production. Potatoes contribute 4 and 5 times more than rice and wheat respectively to the Indian GDP and crop losses including management losses are estimated at approximately Rs. 2600 crores annually, therefore, any sudden disruptions due to epidemic late blight disease of potato affect not only the country's food security but also regional and especially, rural socio-economics even leading to farmer suicides, as seen in the recent past in India (Fry, 2016; Dey *et al.* 2018). West Bengal is a major contributor to the potato production kitty of India, and like elsewhere in the world, the vagaries of the late blight epidemic have affected the policies and human affairs in the state as exemplified by the epidemic of 2013-14. To stem the price rises due to the unavailability of potatoes,

a slew of policy measures was initiated by the government, *viz.* stopping exports of potatoes to neighbouring states like Orissa, etc., which in turn kick-started cultivation in the neighbouring states, and 10 years later in 2023, traders from Bengal were protesting that they were facing difficulty in selling their produce to neighbouring states.

Over the past 180 years, extensive efforts have focused on developing resistant cultivars of *Solanum tuberosum* to counter the disease (Nowicki *et al.* 2012). Despite discovering several resistance (R) genes in wild Solanaceous relatives, achieving durable resistance to the pathogen has remained challenging (Leesutthiphonchai *et al.* 2018; Paluchowska *et al.* 2022). Like other plant pathogens, *P.infestans* employs effector proteins to facilitate colonization of host plants (Andersen *et al.* 2018; Vleeshouwers *et al.* 2011). Many of these effectors contain a specific amino acid motif known as the RXLR motif (Arginine– Any Amino Acid– Leucine Arginine) (Wawra *et al.* 2017). In response, host plants have evolved R proteins that recognize these RXLR effector proteins, triggering an immune response that halts disease progression (Andersen *et al.* 2018; Vleeshouwers *et al.* 2011). Effectors recognized by R genes are referred to as “avirulence factors,” and this gene-for-gene response system accounts for the specific resistance of certain host genotypes against distinct pathogen strains (Flor, 1942).

Despite the tremendous developments and their application in agriculture, *Phytophthora infestans* still threaten potato and tomato production worldwide, necessitating using expensive fungicides for management (Fry *et al.* 2015; Ristaino *et al.* 2020). What is interesting is that while 180 years of unfettered devastation should have made it an almost familiar pathogen, about whom much is expected to be known, and which we should be able to defeat, and yet, it continued to devastate crops since 1843 in a seeming conundrum begging the question, do we not ‘*know thy enemy*’? The answer perhaps lies in the inadequate incorporation of the diversity of its genome into disease management perspectives to date.

The pathogen relies on its genome architecture driven by a repeat and transposon-driven

expansion giving rise to a 'two-speed genome' (Haas *et al.* 2009) to provide for a wide repertoire of ever-changing effectors enabling it to become a reemerging pathogen across the years (Fry *et al.* 2015). *P. infestans* has several genotypically defined clonal lineages and sub-clonal lineages (Cooke *et al.*, 2012; Dey *et al.* 2024) that rapidly evolve continuously, bringing about a varied and unstable temporal and spatial distribution worldwide. Quick detection of these changing 'variants' in real-time is the key to control and countermeasures, as the lineages in addition to differing genotypically, often have different phenotypic characteristics in the field which affect the pathogen's ability to cause epidemics. Epidemics are not caused by a single pathogen but rather by multiple variants or populations of pathogens, each with distinct capabilities. To effectively combat these 'variants of concern,' it is crucial to identify and understand their unique characteristics and enhanced abilities. The variants arise through selection pressure-driven co-evolution leading to the breakdown of the R gene-mediated host resistance, higher aggressiveness, fungicide resistance and ability to adapt to varying environmental conditions (Haas *et al.* 2009; Cooke *et al.* 2012; Dey *et al.* 2018; Fry, 2020; Dey *et al.* 2024).

Migration of such newly evolved genotypes/lineages to a new geographical area through trade, natural imports or even engineered distribution could trigger an epidemic. This has been evidenced by different studies throughout the world including India (Goodwin *et al.* 1994, Cooke *et al.* 2012; Fry *et al.* 2013; Chowdappa *et al.* 2015; Dey *et al.* 2018; Guha Roy *et al.* 2021; Dey *et al.* 2024). The answer therefore lies in understanding the variability of the *Phytophthora infestans* populations as it is directly related to its disease or epidemic-causing ability. Understandably, thus the key is to detect the variation in the pathogen population and integrate that information to manage the pathogen. This can be done by monitoring the changing nature of this pathogen through a study of the population structure, by continuous nationwide surveillance, and accordingly updating the management strategy. Determining the population structure and studying diversity is the logical first step for any plant pathogen population because these studies

reflect the pathogen's fundamental biology, phenotypic characteristics, genetic composition, evolutionary history, and its dispersal: aspects important for formulating management strategies. The oldest characterised late blight specimen from India is about 111 years old from Bhagalpur in 1913 belonging to the FAM-1 lineage, the same clonal lineage of *P. infestans* that caused the Irish Potato Famine, which was subsequently replaced by the US-1 genotype around 1968-74 (which originated in the US in the 1930s–1950s) in India (Saville and Ristaino, 2020). Since then, three landmark incidents have happened in Late blight (LB) populations in India, one, the detection of A2 populations in 1986, second, populations resistant to the fungicide metalaxyl (the most popular fungicide against LB) were found in 1989, and the identification of the migratory European 13_A2 populations in 2008 from South India. (Guha Roy *et al.* 2021) all of which had rendered the extant disease management strategies ineffective. The current dominant Indian population which has replaced all the older populations is the migratory European 13_A2 which has already caused three epidemics in India and has been extensively studied by the author's group since 2009. (Dey *et al.* 2018; Guha Roy *et al.* 2018, 2019, 2021, 2022 ; Dey *et al.* 2024).

The 13_A2 is an asexually propagated clonal lineage, yet shows extensive diversity, both genotypic and phenotypic making it a management challenge across potato growing regions in India. The Indian populations have a unique attribute not seen elsewhere. Even though the population was clonal, the pathogen population (sub-clonal lineages based on genotyping by standard SSR markers) were broadly more aggressive on potatoes than on tomatoes and could accordingly grouped into three groups; one more pathogenic on potatoes, another on tomatoes and the third equally on potato and tomato (Dey *et al.* 2018). These differences in aggressiveness on potatoes and tomatoes affect disease outbreaks and management. Knowing the identity of the clonal lineage therefore becomes important to schedule sprays in a potato or tomato field; for a tomato-aggressive clonal lineage in a potato field, fewer sprays would be needed, translating to lower input costs for the farmer.

The current LB Indian population is the 13_A2 which though a migratory clonal lineage from temperate Europe, has been very successful in establishing itself in tropical Asia, especially India and Bangladesh (Guha Roy *et al.* 2021). These sub-clonal lineages have developed local adaptations to higher temperatures, enabling robust mycelium growth across a broader temperature range (12-25°C). This adaptation supports sustained growth and allows sporulation to occur at temperatures up to 25°C. As a result, the pathogen's epidemic potential increases, extending the disease window period for infection, particularly affecting potatoes and tomatoes cultivated during winter in the tropical plains. (Guha Roy, 2019). Potatoes are grown in the Gangetic plains during winter and harvested depending on the region from February to March. The weather conditions are typically favourable for LB after the onset of western disturbances around the end of January to early February in Bengal when the temperatures are low, after which the temperature rises and the favourable disease window for LB onset fades. However, these thermotolerant sub-clonal lineages would still have a favourable disease window even later in February (during higher temperatures) if other weather conditions are met, which necessitates a change in current management strategies. As regards fungicide sensitivity, the older Indian LB populations were differentially resistant to the most used fungicide metalaxyl. All the sub-clonal lineages of the 13_A2 clonal lineage are resistant to the fungicide metalaxyl and its use must be stopped immediately. However, the 13_A2 populations are also showing a differential sensitivity and in some cases reduced sensitivity to the five commonly used commercial late blight targeted fungicide formulations, namely mancozeb (Indofil M-45®, 75% a.i.; Indofil Industries Limited, India), azoxystrobin (Amistar®, 23% a.i.; Syngenta), dimethomorph (Acrobat®, 50% a.i.; BASF), fosetyl-Al (Aliette®, 80% a.i.; Bayer crop Science), and a blend of two fungicides mancozeb + cymoxanil (Curzate M-8®, 64% + 8% a.i.; DuPont) (Unpublished).

These changed field attributes of host-adapted clonal lineages, fungicide-insensitive and thermotolerant LB populations necessitate change in current spraying schedules and management strategies. However, it must be understood that these attributes are dynamic in

time and therefore continuous surveillance of LB populations is necessary for effective disease management.

In addition to the above studies on field attributes, further studies of the population dynamics of Indian LB populations at the sub-clonal level during epidemic and sporadic years across large and diverse potato-growing regions in India were done for investigation of any temporal maintenance of locally adapted multilocus genotypes (MLGs) in the author's laboratory (Dey *et al.* 2018, 2024). These unique MLGs within a clonal population were derived from genotypic diversity studies using 12-plex simple sequence repeat (SSR) markers that can be considered synonymous with the sub-clonal lineages. The LB pathogen population diversity was higher in regions around the international borders with Bangladesh and Nepal. Overall, the multiple shared MLGs suggested genetic contributions from the UK and Europe and a sub-structure based on the geographical location within India. Samples from West Bengal were the most diverse and grouped alongside MLGs found in Europe, the UK and neighbouring Bangladesh but were not linked directly to most samples from south India. (Dey *et al.* 2018). After the first detection of 13_A2 in India due to the epidemic in South India in 2008, increasing levels of sub-clonal variation were tracked over time and space across India and 115 sub-clonal lineages have been detected from India, out of which 90 are unique to India. In India, a regional pathogen population structure was observed with evidence for local migration, cross-border movement between surrounding countries, and introductions via imports. There was also evidence of genetic drift and between-season transmission of more strongly pathogenic subclones with a complete displacement of some sub-clonal types. The limited introduction of novel genotypes and the use of resistant potato cultivars could contribute to the dominance of the 13_A2 lineage. (Dey *et al.*, 2024). The most important factor for population changes and resultant epidemics in Asia, especially India, is the migration of pathogen genotypes from Europe and the Americas. Reducing the impact of such migration in the future will necessitate putting in place improved phytosanitary measures and continuous surveillance, tracing, tracking, and charact-

erization of the pathogen strains to effectively manage the late blight disease in India (Guha Roy *et al.* 2021).

To achieve this, international cooperation and funding for data sharing using global networks similar to funding structures such as those in place for wheat blast (Latorre *et al.* 2023) is required. Towards this objective, the International Potato Center (CIP), Peru, which is an International Organization [as per the agreement for the recognition of the international legal personality of the International Potato Center, duly registered with the Secretariat of the United Nations under Art 102 of the UN Charter (with registration number No. 55040)] and a member of the CGIAR System Organization is an international entity with the mandate for potato, sweet potato, and Andean root and tuber crops, has formed a worldwide network for LB. Surveillance networks for LB like Euroblight (for Europe <https://agro.au.dk/forskning/internationale-plaetform/euroblight/>), USABlight (for USA <https://usablight.org/>), Tizon Latino (for South America <https://tizonlatino.wordpress.com/>) and Africa Blight (for Africa) are being utilised for crop protection and the prevention of epidemics. The USABlight was initially created with funding from USDA's Agriculture and Food Research Initiative (AFRI) and is now a valuable resource for LB management in the USA. The Euro Blight is a unique collaborative platform which is a very active multi-disciplinary, multi-actor consortium and network launched with initial funding from the EU. Both the USABlight and the EuroBlight are implementing surveillance of LB populations to manage the LB effectively in these regions. The TizonLatino is a network of 10 South American countries and the AfricaBlight is yet to take off fully. Asia Blight (for Asia) was a late entrant to these efforts and is mentored by the CIP, Peru, however, currently, it is well-organised with 15 member countries. The author is a regional representative for India and a member of the scientific committee of AsiaBlight. Besides these networks, regional centres like the International Potato Center – China Center for Asia Pacific (CIP-CCCAP), Beijing, China and the proposed CIP-South Asia Regional Centre (CIP-SARC), Agra, India are further expected to strengthen these efforts. Additionally, crop loss and

biosecurity concerns have led to well-established monitoring centres for continuous bio surveillance established by advanced economies worldwide, except India. China for example already has 900 monitoring stations for LB (Cooke *et al.* 2022), therefore in the Indian context, there is an urgent need to establish an epidemic-surveillance network and infrastructures in the national interests of food and biosecurity of the nation.

DECLARATION

Conflict of Interest. Author declares no conflict of interest

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