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REVIEW

LATE BLIGHT DISEASE OF POTATO AND ITS MANAGEMENT

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ABSTRACT: Late blight caused by *Phytophthora infestans* is one of the most dreaded diseases of potato worldwide and cause significant loss in production. The pathogen is highly variable and adapt to the newly bred varieties and fungicides. Population of *P. infestans* in most of the countries has changed dramatically and original A_1 has almost been displaced by more virulent A_2 strain. In India, A_2 mating type was recorded in 1990s and now it has displaced the A_1 in temperate highlands while in sub-tropical plains still A_1 is dominating. Virulence to all major resistance genes has been recorded and in India the racial complexity has reached to its zenith resulting in breakdown of many disease resistant varieties. Indiscriminate use of metalaxyl based fungicides has led to the development of metalaxyl resistance world over including India, which has necessitated the use of additional systemic molecules for the management of this disease. The population of *P. infestans* characterized using molecular markers has led to better understanding of pathogen at molecular level. Mitochondrial DNA haplotyping of *P. infestans* has revealed that mt Ia is displacing the other haplotypes globally at a faster rate including India. Relationship between *P. infestans* and the weather is well understood and has been utilized for developing disease forecasting models and decision support systems across the globe including India. An increasing severity of late blight in many potato growing areas, a shift in pathogen population toward increased specific virulence and an increasing tolerance to the most effective late blight specific fungicides suggests a need to develop an appropriate disease management strategy based on information technology.

KEYWORDS: *Phytophthora infestans,* pathogen variability, epidemiology, forecasting

Late blight caused by oomycete *Phytophthora infestans* (Mont.) de Bary has historically been an important disease of potatoes and tomatoes worldwide. In the mid 1800, late blight caused widespread crop failures throughout Northern Europe including Ireland where it was responsible for the Irish famine (Elansky *et al*., 2001). Since then, it has spread far and wide and now occurs wherever potatoes are grown. Losses due to *P. infestans* have been estimated to € 12 billion per annum of which the losses in developing countries have been estimated around € 10 billion per annum (Haverkort *et al*., 2009). A survey carried out to estimate the impact of late blight on potato yield and fungicide use in the United States revealed that use of the fungicides alone cost $77.1 million at an average cost of around $507 per ha which do not include non-fungicide control practices (Guenthner *et al*., 2001). Region wise economic importance of late blight shows that the disease takes highest toll of potato in Sub-Saharan Africa (44% crop losses) followed by Latin America (36%), Caribbean (36%), South-East Asia (35%), South-West Asia (19%) and Middle East and North Africa (9%) (CIP, 1997). Information on various aspects of late blight has been reviewed by different workers (Erwin *et al*., 1983; Neiderhauser, 1986; CIP, 1989; Ingram and Williams, 1991; Singh and Shekhawat, 1999; Singh and Bhat, 2003; Fry, 2008; Cooke *et al*., 2011; Lozoya-Saldana, 2011).

SYMPTOMS

The disease appears as water- soaked irregular pale green lesions mostly near tip and margins of leaves which rapidly grow into large brown to purplish black necrotic spots. A white mildew, which consists of sporangia

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and spores of the pathogen, can be seen on lower surface of the infected leaves especially around the edges of the necrotic lesions. Light to dark brown lesions encircle the stems. The affected stems and petioles become weak at such locations and may collapse. Entire crop gives blackened blighted appearance especially under disease favourable conditions and may be destroyed within a week. Tubers in soil become infected by rain borne sporangia coming from the diseased foliage. Late blight infected tubers show irregular reddish brown to purplish areas which extend into internal tissues of the tubers. The infected tubers usually are hard, dry and firm but may get attacked by soft rot causing bacteria and rot in field and stores.

THE PATHOGEN

Late blight is caused by *Phytophthora infestans* (Mont.) de Bary. It belongs to the oomycetes, a diverse group of eukaryotic microorganisms in a group called the Stramenopiles, clustering together with others in a super group, the Chromalveaolata (Adl *et al*., 2005). The position of the oomycetes as a unique lineage of eukaryotes unrelated to true fungi but closely related to heterokont (brown algae) and diatoms which is well established through molecular phylogenies and biochemical studies (Baldauf *et al*., 2000).

PATHOGEN VARIABILITY

Monitoring population structure of *P. infestans* has been on the agenda of scientific community and new techniques have become available. Earlier biological markers including mating types, race pattern and metalaxyl sensitivity were used for monitoring the population structure of *P. infestans.* But now with the introduction of molecular techniques, other markers have gained importance. The most used techniques for late blight population studies are: Isozymes, RFLP (restriction fragment length polymorphism), mitochondrial haplotype, AFLP (amplified fragment length polymorphism) and, SSRs (simple sequence repeats, microsatellites) (Cooke and Lees, 2004).

Physiological races: *Phytophthora infestans* is highly variable. The variability in the pathogen is evident by the frequent appearance of its new pathogenic types (virulences) in field and sectoring of fungus colonies often observed in the laboratory. Giddings and Berg (1919) and Berg (1926) were pioneers in detecting variations in the *P. infestans* populations. Pathological specializations (races) within potato isolates were reported by Schick (1932) after almost seven years of introduction of resistant hybrids/cultivars having R genes. However, universal appearance of races or, at least their detection, did not occur until resistance genes from *Solanum demissum* were transferred to commercial potato species, *S. tuberosum*. Since then, race spectrum in different countries/regions has been monitored regularly. One hundred and twenty one races were reported from Mexico (Rivera-Pena, 1995). Thirty eight physiological races were identified among 60 potato and tomato isolates from different Italian regions (Cristinzio *et al*., 1998). Virulence to all major resistance genes was recorded (Guo *et al*., 2009) and 61 races were detected in northern China (Li *et al*., 2009) and Estonia (Runno *et al*., 2009). In India, the racial complexity has reached its zenith and presently most complex races (10-11 gene complex) are prevalent in most potato growing regions (CPRI, 2013).

Mating types: *P. infestans* is heterothallic and requires two mating types for sexual reproduction. Prior to 1984 the A_2 mating type was restricted to Mexico and Andean mountains which is the centre of origin of cultivated potatoes. First report of A_2 mating type outside Mexico was from Switzerland (Hohl and Iselin, 1984). Subsequently, A2

mating type was detected in USSR during 1990s (Vorobev *et al*., 1991), USA (Deahl *et al.,* 1991), Belarus (Ivanyuk and Konstantinovich, 1999), Netherlands (Drenth *et al*., 1993), India (Singh *et al*., 1994), Pakistan (Ahmed and Mirza, 1995), Northern Ireland (Cooke *et al*., 1995), Canada (Chycoski and Punja, 1996), France (Gilet, 1996), China (Zhiming *et al*., 1996), Hungary (Bakonyi and Ersek, 1997), Italy (Cristinzio and Testa, 1997), Ecuador (Oyarzun *et al*., 1997), Myanmar (Myint, 2002), Colombia (Vargas *et al*., 2009) and Sri Lanka (Kelaniyangoda, 2011).

Occurrence of A_2 mating type in different parts of the world is considered to be due to a second migration of *P. infestans* from Mexico (Fry *et al*., 1999), the first being from Europe and America during the historical potato famine around the year 1845. Despite introduction of A_2 mating type in different parts of the world through migrations, its further build-up vis-à-vis the old population (A_1 mating type) has not followed a definite trend. In Sweden (southwest), Hungary and Estonia both mating types were detected (Widmark *et al*., 2007; Nagy *et al*., 2006; Runno *et al*., 2009). In Mexico (Michoacan) both A_1 and A_2 mating types were detected in equal ratio in the same field (Fernandez-Pavia *et al*., 2005). Majority of the isolates collected from China (Guo *et al*., 2009; Li *et al*., 2009) and Southern Germany had only A_1 mating type (Moller *et al*., 2009). However, in most of the countries the new strain has already taken over or is fast displacing the old strain (Spielman *et al*., 1991). In India, A_2 mating type has stabilized in temperate hills while the A_1 is dominating in sub-tropical plains (Singh *et al*., 2005; CPRI, 2013). The new strains of the pathogen have been found to be more aggressive than the old population (Fry *et al*., 1999). Turkensteen and Mulder (1999) have reported that pathogen during the last 20 years has developed a shorter life cycle (by 30%), ability to cause more leaf spots, shorter infestation period (6 instead of 8h), tolerance to a greater temperature range (5 to 27^0 C instead of 10 to 25 ^{o}C), form stem lesions more frequently, develops oospores and sporulation on tubers and is more inclined to develop resistance to fungicide metalaxyl.

Population of *P. infestans* in most countries has changed dramatically and original A_1 have almost been displaced by more virulent A_2 strain. Occurrence of both A_1 and A_2 strains at the same location has also opened up the possibility of development of thick walled oospores which could survive extreme winter (Medina and Platt, 1999) or summer conditions. The oospores may act as another source of primary inoculum, in addition to the already known sources such as infected seed tubers, waste heaps and volunteer plants etc. The impact of potato late blight increased greatly during the 1990s following the migration of more genetically diverse and more aggressive genotypes of *P. infestans* from Mexico (Goodwin *et al*., 1994). Recent work has indicated that the new *P. infestans* clones, especially the US-8 and US-14 genotypes, are more aggressive (Lambert and Currier, 1997; Kirk *et al*., 2001; Kirk *et al*., 2009). The new genotypes of late blight are 10 times more likely to produce infected sprouts than their predecessor, US-1 (Marshall and Stevenson, 1996). Migration and sexual recombination can play an important role in enhancing genetic diversity in *P. infestans*. Chowdappa *et al*. (2013) have recently reported that migration of 13_A2 genotype was responsible for outbreak of destructive late blight epidemics in Karnataka state of India since 2009 and has suggested the importance of bio-security in agricultural trade. An increasing severity of late blight, a shift in pathogen population toward increased specific virulence and an increased tolerance to metalaxyl has been recorded in past three decades in the north western plains of India (Arora, 2008)

Metalaxyl resistance: Metalaxyl a phenylamide group of systemic fungicide was highly effective against *P. infestans* and other peronosporales and was used worldwide to combat mildews and *Phytophthora* diseases of various crops**.** It is taken up rapidly by almost all parts of potato plant, translocate acropetally and exerts its fungitoxic effect only inside the host tissue. Its effectiveness was so remarkable that it suppressed lesion appearance, enlargement and sporulation in low concentrations (10-25 ug/ml) and was effective even when used as curative after three days of inoculation (Urech *et al*., 1977). Metalaxyl acts by interference in RNA synthesis by inhibition of rRNA polymerase or both RNA and DNA synthesis. Its site specific nature made it more prone to development of resistance in the pathogen. Fungicide resistant isolates were detected in oomycetous fungi soon after the introduction of these fungicides as single products on various crops including *P. infestans* in Europe (Carter *et al*., 1982; Cooke, 1981; Davidse *et al*., 1981; Dowley and O'Sullivan, 1981), the Middle East (Cohen and Reuveni, 1983), and in the Moscow region at the end of 1980's (Elansky *et al*., 1999). In India, resistance to metalaxyl in *P. infestans* wild population was first observed in Nilgiri hills of South India in 1989. Metalaxyl resistant strains appeared towards the end of summer crop season and their frequency increased to 13 per cent in autumn season. Field trials carried out between 1989 to 1992 indicated that the metalaxyl + mancozeb mixture could best be used from early to mid summer and must be avoided toward the end of summer season or during the autumn season when the resistant isolates were more frequent in the region (Arora *et al*., 1992). Since then the monitoring for metalaxyl tolerance is being done regularly. In Hungary 60% isolates have been reported resistant to metalaxyl (Nagy *et al*., 2006) while in Estonia all three categories i.e. resistant, intermediate and sensitive were found (Runno *et al*., 2009). Similarly, majority of isolates from southern Germany (Moller *et al*., 2009) and China were found resistant to metalaxyl (Li *et al*., 2009). To prolong the effectiveness of fungicides liable to encounter resistant problems Fungicidal Resistance Action Committee (FRAC) of International Group of National Associations of Agrochemical Manufacturers (GIFAP) has set up country specific working groups for phenylamide fungicides. A few strategies have been identified to manage the problem of resistance against metalaxyl in *P. infestans*. These include withdrawal of straight product and introduction of mixture with contact residual fungicides, regulation of number of sprays and their use early in the season, etc.

Ploidy: Polyploidy is known to play an important role in the evolution of higher plants and animals (Stebbins, 1971; Lewis, 1980) but its role in the evolution of fungi has been emphasized by some and dismissed by others (Maniotis, 1980). Although polyploidy has been found to occur in true fungi (Rogers, 1973) and oomycetes (Win and Dick, 1975), the biological relevance of polyploidy and its role in evolution of these groups remain obscure. In *P. infestans*, polyploidy, as measured using Feulgen-DNA cytophotometry, appears to be quite common in populations outside Mexico. Sansome (1977) speculated that polyploids could have arisen by selection of auto-tetraploid nuclei that may occasionally arise during periods of rapid nuclear divisions. Conversely, allopolyploid could have arisen by chromosome doubling in hybrids between *P. infestans* and other species (Sansome, 1977). Ploidy status in India revealed that *P. infestans* population consisted of diploids, triploids and tetraploids. A_1 mating type isolates were predominantly diploids (50%) followed by triploids (33%). Sub-tropical *P.*

infestans population (A_1 mating type) was predominantly diploid and tetraploid (40% each). Frequency of different polyploids in A_2 type strains was equal (Singh *et al.*, 1997). Studies on sexual compatibility amongst different polyploids revealed that isolates of the same ploidy status mated freely i.e. diploid x diploid or tetraploid x tetraploid whereas those with varying ploidy status did not mate frequently indicating that sexual reproduction in nature would be conditioned by the ploidy status of the *P. infestans* genotypes. The polyploids differed in their aggressiveness. Preliminary investigations revealed that diploids of A1 mating type are more aggressive than triploids. This trend was however not observed in polyploids of the A_2 type (Singh *et al.*, 1997).

Isozymes: Isozymes have proved to be useful markers to estimate levels of genetic variability in populations, to study species dispersions, and to conduct phylogenetic analyses. Glucosephosphate isomerase (*Gpi*) and peptidase (*Pep*) are two systems for which simple genetic control has been demonstrated (Shattock *et al.*, 1986; Spielman *et al.*, 1990). Allozyme genotypes are described in terms of relative mobilities of their bands of activity during electrophoresis. The most common allele is assigned a mobility of 100 and other alleles are assigned a number based on their relative mobility. Thus 90/100 refers to a heterozygous genotype with two alleles, one allele being the most common type, and the other producing an enzyme that migrates 90% as far as the common type (Fry *et al.*, 1991). The 90 allele for *Gpi* and the 83 allele for *Pep* were detected only in Europe for the first time after detection of the A_2 mating type: the changes in allozyme alleles occurred concomitant with the change in mating type structure (Spielman *et al.*, 1991). Isolates of the A_2 mating type and new allozyme genotypes were discovered in the Netherlands and East Germany as early as 1980 (Daggett *et al.*, 1993; Drenth *et al.*, 1994). Studies of isolates collected in Ireland in 1988 and 1989 showed that they belonged to the new population: the allozyme genotypes *Gpi* 90/100 *Pep* 83/100; *Gpi* 90/100 *Pep* 100/100; *Gpi* 100/100 *Pep* 83/100 and *Gpi* 100/100 *Pep* 100/100 were detected which are characteristic of the new population (Tooley *et al.*, 1993). The genotypes US-1 and US-8 are exceptions to the general rule of diploidy in *P. infestans*; individuals with these genotypes are probably 2n +1, having an extra copy of the chromosome that contains the *Gpi* locus. US-1 probably has two copies of the 100 allele and one of the 86 allele. US-8 probably has three different alleles at the *Gpi* locus: 100, 111, and 122 (Goodwin *et al.*, 1992). This would give a six-banded phenotype on a gel, with three homodimer (100/100, 111/111, and 122/122) and three heterodimer (100/111, 111/122, 100/122) bands. However, the 111/111 homodimer and the 100/122 heterodimer bands co-migrate, so only five bands are resolved on the gels (Goodwin *et al.*, 1995). US-6 genotype has a *Gpi* banding pattern 100/100, US-7 has 100/111, US-11 has 100/100/111, US-10 has 111/122, and US-17 has 100/122 (Goodwin *et al.*, 1998). As for *Pep*, US-1 and US-6 have bands 92/100; US-7, US-8, US-11, and US-17 have genotype 100/100. In India, *P. infestans* population has been analysed for *Gpi* since 1998. All of the isolates across the country were monomorphic as only single band was resolved. This makes the *P. infestans* Indian population distinct from European and American populations. It is closer to Peruvian population which is also monomorphic for *Gpi* (Singh and Shekhawat, 1999). In Hungary all isolates were monomorphic at the *Gpi* locus but four allele combinations were found at the *Pep* locus (Nagy *et al.*, 2006). Allozyme analysis did not reveal any polymorphism in Estonian population (Runno *et al.*, 2009) while different banding patterns were observed

for *Gpi* with dominant banding pattern of 100/100/111 whereas all isolates tested were homozygous (100/100) at the *Pep* locus in Chinese population (Li *et al*., 2009). Similarly, different banding patterns were observed for both *Gpi* and *Pep* loci in Mexican population (Fernandez-Pavia *et al*., 2005).

Mitochondrial haplotypes: Mitochondrial DNA variation may be more useful than nuclear DNA variation for studying the migration events in *P. infestans,* since these variations evolves rapidly, uniparentally inherited and no segregation, elimination, or recombination of haplotypes have been observed in such variations (Klimczak and Prell, 1984; Forster *et al*., 1990; Carter *et al*., 1990). Molecular analyses of specific genes from mtDNA have been used to establish evolutionary relationships in the genus *Phytophthora* which demonstrated that *Phytophthora* species were distinct from true fungi (Forster *et al*., 1988; Forster *et al*., 1990). Mitochondrial haplotypes have been designated in *P. infestans* using both PCR approaches and RFLP analysis of mitochondrial DNA (Carter *et al*., 1990; Griffith and Shaw, 1998). A research group in Bangor, Wales identified haplotypes Ia, Ib, IIa, and IIb (Griffith and Shaw, 1998).

May and Ristaino (2004) analysed the herbarium specimens collected during the Irish potato famine and later in the 19th and early 20th century and found that 86% of the specimens were infected with Ia mtDNA haplotype which was responsible for the historic epidemics during the 19th century in the UK, Europe and the USA. The *P. infestans* mtDNA derived from 10 historic herbarium samples lacked the variable mtDNA region found in modern Ib haplotypes (Ristaino *et al*., 2001)**.** Thus, present theories that assume the Ib haplotype is the ancestral strain responsible for the Irish famine are incorrect and need to be re-evaluated (Fry and Goodwin, 1997; Goodwin *et al*., 1994). In India, all isolates studied since 2002 were of the Ia mtDNA haplotype (except those from the north-east Shillong hills). It seems likely that the Ib haplotype has been displaced by the Ia haplotype, however three isolates reported as IIb mt DNA haplotype (Chimote *et al*., 2010) were the same as have been previously reported from Mexico, western states of the USA, Canada (Goodwin *et al*., 1994; Gavino and Fry, 2002) and Nicaragua (May and Ristaino, 2004). Ia haplotype dominance (92%) was also reported in Polish population of late blight isolates (Chmielarz *et al*., 2010). General tendency of Ia haplotype domination is common in most of Europe, with exception of Northern Ireland where a IIa haplotype is more frequent (Chmielarz *et al*., 2010). The recent study in Chiang Mai and Tak provinces of Thailand between 2006 and 2009 showed the dominance of IIa haplotype (Jaimasit and Prakob, 2010). The mt-DNA haplotype of isolates collected from Heilongjang and Jilin Provinces were determined as two genotypes, Ia and IIa, of which 11.1% isolates were Ia and 88.9% isolates were IIa (Xuanzhe and Shengjun, 2010). However, a previous study in five provinces of Northern China between 1997 and 2003 revealed the 100% dominance of IIa haplotype (Guo *et al*., 2009). The Ia haplotype was found during the first outbreaks of the disease in China (1938 and 1940), Japan (1901, 1930 and 1931), India (1913), Peninsular Malaysia (1950), Nepal (1954), The Philippines (1910), Australia (1917), Russia (1917) and Latvia (1935) (Guo *et al*., 2010). Before 1980s, worldwide populations of *P. infestans* were dominated by a single clonal lineage, the US-1 genotype with Ib mtDNA haplotype (Goodwin *et al*., 1994). This lineage has since been displaced by the other haplotypes (Ristaino *et al*., 2001). Since 2002, in India most isolates studied

were of Ia mtDNA haplotype (Chimote *et al*., 2010). Displacement of old Ib mtDNA haplotype population by new Ia haplotypes is consistent with the global trend of mt haplotype distribution.

EPIDEMIOLOGY

Prior to germ theory, potato late blight was attributed to bad weather. However, later on, it was established that a fungus, *Phytophthora infestans* affects the potato crop with lightning speed under wet conditions causing this disease. Ambient temperature, RH, light, fogginess, rainfall, dew, wind velocity etc. were found to have a strong relationship with the blight pathogen and the disease.

Effect of environment on the pathogen

Spore production: The optimum temperature for fungus development is 16-24°C. Sporangia are usually produced between 8.5 and 26°C with an optimum of 19-22°C (Vowinekel, 1926). Abundant sporangia are formed at low air speed when the ambient humidity is 90-100% RH (Crosier, 1934). At higher air speed, numerous sporangia are formed even at 100% RH. Sporulation is encouraged by high humidity close to foliage associated with surface moisture. Sporulation in the field is inhibited by light during the day, a feature that ensures that sporangia are formed only at night when humidity and temperature conditions favourable for the sporulation. Low intensity of blue light (peak 450 nm) is strongly inhibitory and the inhibition increases with an increase in the temperature from 10 to 25° C (Cohen *et al*., 1975).

Oospores, the sexually produced resting spores are formed where both mating types A_1 and A_2 coexist. Temperatures in the field are generally conducive for the oospores production in most potato growing areas. These are produced at temperatures ranging from 8-22° C with an incubation period of 7-14 days (Harrison, 1992). Studies carried out in the laboratory revealed that the oospores are also produced freely when *P. infestans* is grown in constant darkness and a few or no oospores are formed under continuous illumination with light from white fluorescent or incandescent lamps. Irradiation with red light (> 600 nm) encourages oospore formation (Harnish, 1965). High moisture content of the host tissue (Ý88%) and low ambient RH (50-54%) favoured oospore formation under controlled environment. It took 14-16 days for oospore to develop; thereafter the number of oospores increased with time and decreased with moisture content of host tissues (Singh *et al*., 2004).

Spore germination: Duration of leaf wetness, inoculum density, temperature and their interactions determine spore germination and infection on potato plants. Sporangia and zoospores germinate only in the presence of free water. Zoosporangia germinate either indirectly by releasing zoospores or directly by producing a hyphal outgrowth. Sporangia release zoospores at low temperatures (4-12°C), while at higher temperatures (15-27°C), it germinates directly by producing the hyphal outgrowth (Rotem *et al*., 1971). Longer period of leaf wetness are required for germination, if the temperature deviates from the optimum (Harrison, 1992). A low intensity irradiation (300-390 nm wave length) increases the proportion of sporangial germination, while high intensity irradiation kills the spores (De Weille, 1963).

Oospores germinate at temperatures of 12 to 25°C by producing one or two short germ tubes bearing a terminal sporangium which either germinates directly or indirectly by liberating the zoospores (Smoot *et al*., 1958). They germinate only in water or dilute aqueous solutions and are tolerant to environmental extremes. They do not

germinate in continuous darkness but the short daily exposure to moderate light intensity from fluorescent lamp stimulates germination. These resting bodies germinate well under continuous irradiation of blue light (430-490 nm) (Shattock *et al*., 1986).

Pathogen survival: Mycelium of *P. infestans* can tolerate considerable variation of humidity and temperature within the potato plants but sporangia are unable to survive temperatures above 25°C for more than 84h. However, these are able to survive adverse ambient conditions when they are in contact with leaf surface, presumably because transpiration ensures the air surrounding them is close to saturation (Rotem and Cohen, 1974). Without a film of water, sporangia lose viability within 5 and 2.5 min at 95 and 90% RH, respectively. UV component of sunlight is an important factor in reducing the viability of detached sporangia. Exposure to solar radiation is also the main cause for death of dispersed sporangia during the daytime. Thick walls of oospores enable them to resist drying. Oospores in nature are either embedded in the host-plant tissues or buried in the soil, and as such these are rarely exposed to dry air.

Effect of environment on host

Growth and development of host plants influence development of late blight. Young plants are highly susceptible to blight while plants of intermediate age are more resistant than the young or old plants (Lowings and Acha, 1959). Leaflets of plants at flowering stage are most likely to give a hypersensitive reaction. Resistance of leaves to infection by *P. infestans* increases, as plants become water stressed and the rate of lesion expansion are strongly correlated to plant age (Carnegie and Colhoun, 1980). Generally potato plants growing under short days are more susceptible to blight than those growing under long days.

Effect of environment on the disease

Infection process: Both sporangia and zoospores can start fresh infection on host plants. Infection by direct germination of sporangia takes longer time as compared to the infection through zoospores. Zoospores remain motile up to 22 h at 5-6°C, whereas at higher temperature (24-25°C), motility decreases to 19 min only (Melhus, 1915). As soon as the zoospores become non-motile, they encyst and adhere firmly to the leaf surface, germinate and infect the host tissues. Germination of zoospores takes place at 3 to 28° C and germ tube elongation occurs most rapidly at about 21°C (Crosier, 1934). Infection usually occurs within 2.5h of inoculation with the zoospores and small necrotic flecks appear within the next 24-48 h.

Dispersal of sporangia: *Phytophthora infestans* sporangia are formed at night when the humidity is high and disperse in the following morning when there is a rise in temperature and fall in RH. The detachment of sporangia from the sporangiophores on leaves is mainly due to the changes in humidity rather than temperature (Hirst, 1958). Irradiation decreases the RH by heating the air close to the leaf surface, and resulting changes in humidity can affect the sporangial release (Hirst, 1958). Number of sporangia trapped per hour is more closely correlated with radiation than with any other weather factor. Sporangia are hydrophilic and get readily dispersed into water falling on them. Splash droplets containing spores could result in transporting of the pathogen over short distances. Sporangia on the soil surface could also get splashed on to the leaves and initiate lesions development. Soil containing sporangia could remain infective about 3 weeks. Rain washes the sporangia from the infected foliage and the rain water containing the spores usually move along the stems into the soil and infect the tubers.

Development of an epidemic: Temperature between 7 to 27°C is favourable for blight development. Humidity plays a major role in development of an epidemic. Prolonged survival of sporangia requires high RH (Martin, 1923). The magnitude of disease progress depends on an interaction between biotic factors such as cultivar, age, nutrition, the amount of inoculum present on the host and the abiotic factors such as distribution and duration of saturated or near-saturated air within a favourable temperature in the crop canopy. The potential for disease build-up from a single lesion on a leaflet is enormous since 9.8 x 10^5 sporangia are produced over one leaflet of a susceptible potato cultivar in 12 days in saturated air at 15°C (Harrison, 1992). Lower humidity however, slows down the progress of an epidemic by inhibiting sporulation, their viability and the infection process (Easton, 1982).

Development of a potato late blight epidemic is greatly dependent on the presence of free water available from precipitation or dew. Infection cannot occur without free water on the leaf surface. Airborne sporangia rapidly lose their viability in the absence of high humidity and a surrounding film of water. Development of an epidemic is more closely associated with the timing of rain than with total rainfall. Overhead irrigation could also result in outbreaks of this disease (Van Everdingen, 1935).Wind has two opposing effects on the development of an epidemic. In the presence of high moisture the wind help in spreading the disease while at low moisture it retards the disease progress by accelerating the evaporation of surface moisture from the foliage and by drying out of the sporangia.

Photoperiod, light quality and light intensity, as well as the duration and intensity of near UV and IR radiation have a direct effect on pathogen development and host susceptibility. Bright sunshine reduces the ambient relative humidity around the foliage (Harrison and Lowe, 1989). The retarding effect of sunshine on the progress of foliage blight, and in particular its effect on infection, was recognized many years ago and this helped to include 'cloudiness' as one of the important parameters in the early late blight forecasting models.

An understanding of pathogen survival can facilitate in developing the disease management strategies. Infected seed tubers serve as overwintering and the primary source of inoculum (Kirk, 2003). The pathogen overwinters as mycelium in infected tubers, in refuse piles and volunteer plants or over-summer in subtropical zones through tubers kept in cold stores (Pushkarnath and Paharia, 1963; Boyd, 1981). Potato tubers left in the field after harvest and cull potato tubers can produce volunteer plants which can carry over the pathogen to the next season (Zwankhuizen *et al.*, 1998). Latent infection of potato tubers by *P. infestans* has been implied in development of the disease in Ecuadorian highlands (Kromann *et al.*, 2008). Latent infection was demonstrated when the pathogen was detected with the aid of polymerase chain reaction (PCR) in asymptomatic tubers (Appel *et al.*, 2001; Hussain *et al.*, 2005; Hussain *et al.*, 2013). Johnson and Cummings (2009) demonstrated presence of latent infection in seed tubers and production of viable sporangia of *P. infestans* after cold storage of infected potato tubers. Survival of pathogen as oospores in soil serves as another source of primary inoculum. However, its exact role and extent of contribution is not clear. Movement of pathogen from infected tubers to new plant could be indirect through soil. Tubers in soil get infected by contact with sporangia coming from infected haulms through rain water. The infection can also occur during washing of tubers.

DISEASE FORECASTING AND DECISION SUPPORT SYSTEM

Disease forecasting allows the prediction of probable outbreaks and decision support system can help in management of any further increase in disease intensity. This allows us to take strategic decisions about the disease management. Various concepts have been developed and utilized over the years for predicting late blight across the globe. They include 'Dutch rules', Beaumont's periods, Irish rules, moving days concept, severity value accumulation, negative prognosis, mathematical models etc. Van Everdingen (1926) was the pioneer in using weather conditions for forecasting potato late blight under Holland conditions. He used dew periods, night temperature, cloudiness and rainfall, known as the "*Dutch rules*", to predict initial appearance of late blight in Holland. Dutch rules in general were found satisfactory but sometimes the blight would appear even when the 'Dutch rules' were not fulfilled. Subsequently, Beaumont modified these rules for UK conditions and these were known as '*Beaumont rules*' (Beaumont, 1947). These rules were based on specific temperature and RH periods for two consecutive days. They could successfully forecast late blight under UK conditions. However, this concept failed to predict disease in regions where rainfall either did not occur or was erratic during crop period. To overcome this problem Hyre (1954) proposed a concept known as 'moving days concept' which takes care of the break in disease congenial conditions over time. Various workers have further modified this concept from time to time. Wallin (1962) developed 'severity value' concept based on temperature and relative humidity. This system is based on the seasonal accumulation of 'severity values'. Severity values are numbers arbitrarily assigned to specific relationships between duration of RH periods >90% and the average temperature prevailing during those periods. The first occurrence of late blight is predicted 7-14 days in advance after 18-20 severity values have been accumulated. This model has been evaluated extensively worldwide and used by growers in USA and some other countries as well. Besides, mathematical models have also developed to forecast outbreaks of late blight on potato in the south-central area of Washington State, USA (Johnson *et al*., 1996). The concept of 'negative prognosis' was developed by Ullrich and Schrodter (1966) using measurements of temperature, relative humidity, and rainfall to predict when late blight epidemics was not likely to occur. It has been used in Germany and Europe to predict the timing of the first prophylactic spray. Such concept of disease forecasting would be ideal for subtropical conditions since rain and $\geq$ 90 % RH are not so common during the crop season. There are years when such conditions do not occur at all whereas in certain years these conditions occur only for a limited period. Through the use of this model we can avoid the use of excess application of fungicides by calculating the risk values throughout the crop season.

After the development of more powerful computers, a large number of biotic and abiotic factors and their interrelations have been included in forecasting systems and decision support systems have been developed to manage the disease. Although not all these systems have been introduced in practice, still farmers have the option to use these systems in supporting their decision to workout spray schedules. Some of the prominent late blight forecasting systems are discussed below.

BLITECAST: BLITECAST is a computer program that combines two late blight forecasting techniques developed by Hyre and Wallin for forecasting late blight in

USA and Europe (Krause *et al*., 1975). The first part of the program forecasts the initial occurrence of late blight 7-14 days after the first accumulation of either '10 rain-favorable days' according to Hyre's criteria (Hyre, 1954), or the accumulation of 18 severity values according to Wallin's model (Wallin, 1962). The second part of the program recommends fungicide sprays based on the number of rain-favorable days and severity values accumulated during the previous seven days. Fry *et al.* (1983) modified BLITECAST to schedule fungicide applications more precisely once initiation of chemical sprays to manage late blight has begun. They incorporated levels of host resistance and weathering of fungicides with BLITECAST to suit this system for applying chemicals on both susceptible and resistant cultivars.

ProPhy: It was developed in the Netherlands and recommends first fungicide spray when the crop reaches a height of 15 cm in susceptible varieties and ten days later in moderately resistant varieties (Schepers, 1995). A day is considered to be favorable when at least six hours with high relative humidity and at least two hours of leaf wetness or rain are recorded in a period from 8 PM of the previous day until 12 O'Clock on the next day with temperature between 8 to 25 ^{0}C. ProPhy formulates recommendations on the basis of the calculated protection periods and the weather forecast. Results of trials showed that growers using the ProPhy model used fewer fungicide applications than those using a 7-day calendar based model yet they achieved similar disease control (Nugteren, 1997).

NegFry: The model was developed in Denmark and helpful in timing the initial fungicide application and scheduling of the subsequent sprays throughout the growing season. The first part of NegFry is based on the negative prognosis (Ullrich and Schrodter, 1966) that calculates the epidemic free period and then recommends the first spray at the end of this period. The second part of the model is based after the method of Fry *et al*. (1983) which calculates subsequent spraying intervals based on blight units. On an average, this model has been successful in reducing fungicide applications by 50% in some locations. The model has also been implemented in other parts of Europe.

PROGEB: It is an integrated group of forecasting models developed for the main pests of potatoes and cereals in Germany (Gutsche, 1993). One of their components, PHYTEB, forecasts *P. infestans* on potato. PHYTEB consists of two sub-models, SIMPHYT 1 and 2. The first sub-model forecasts the beginning of the epidemics 7 -10 days ahead. It takes into account the cultivars, date of emergence and agro meteorological conditions. The second sub-model simulates the course of the epidemic for two cultivar classes and different fungicide application practices, including no fungicide sprays. Two special features of this sub-model are a detailed mathematical representation of the fungicide's action, and a function to calculate how long fungicide applications can be delayed without any risk.

PhytoPRE: This decision support system was developed in Switzerland (Forrer *et al*., 1993). This model produces three kinds of outputs; *field specific letters* with application recommendations, lists with late blight records and graphs with IP, rainfall and fungicide applications, *weekly bulletins* with late blight records, rainfall, Ullrich and Schrodter's risk values for the whole country, and personal comments from the PhytoPRE manager, and a *lateblight risk map* with IPs for the different regions of Switzerland and all actual late blight records.

Web-blight: In 1996, the Danish Institute of Agricultural Sciences (DIAS) developed a prototype of an Internet based information and decision support system for agriculture. The system was called Pl@nteInfo. Currently this system is in commercial operation in close collaboration between DIAS and the Danish Agricultural Advisory Centre (DAAC). In Pl@nteInfo, comprehensive information and decision support is available for potato late blight such as late blight monitoring and disease forecasting, searchable potato variety database, information about fungicides and control strategies, NegFry homepage, animated weather radar pictures, local weather prognosis etc.(Jensen *et al*., 1996).

Plant-Plus: It was introduced in The Netherlands as a Decision Support System for control of late blight in 1994 (Hadders, 1997). The model is a combination of empirical and fundamental sub-models. Hourly data on temperature, relative humidity, radiation and wind speed are measured in a met station and using this data the model calculates the temperature and leaf wetness in the crop. Together with weather forecasts the critical conditions for development of late blight are calculated. This model recommends sprays by combining the risk for infection with the degree of crop protection. The model has been developed, validated and implemented in the Netherlands.

Guntz-Divoux: This model was developed, validated and implemented in Belgium and France (Goeminne *et al*., 1997). The model calculates the theoretical development of the disease based solely on weather data. Infection occurs when at least 10.5 consecutive hours with RH >90% is measured. The average temperature should be at least 7°C. With these data the models calculates the disease occurrence.

PhytoPRE+2000: It is an internet based decision support system developed in Switzerland and is an improved version of PhytoPRE where weather conditions on major infection and sporulation period (MISP) have been incorporated (Cao *et al*.**,** 1996). Compared to original PhytoPRE programme, it can save about 30-50% chemical usage.

China-blight: A web-based DSS (www.china-blight.net) has been developed in China. This DSS has three sub-systems of "Real-time distribution of potato late blight in China", "Infection risk of late blight pathogen based on measured as well as forecasted weather data" and "A farm based simple DSS for the chemical control on potato late blight". Besides, knowledge information as well as services such as "control methods on late blight", "Resistances of cultivars", "Fungicide database", "Other pests on potatoes", "Questions and experiences exchange" and "Electronic record for field practices of users" has also been included (Hu *et al.*, 2012).

Bio-PhytoPRE: It is a decision support system for organic potato farming. In organic potato production, limited use of copper fungicides is the only means for an effective control of late blight. To avoid negative impacts of copper accumulation in the environment, the Agroscope FAL Reckenholz developed a DSS to assist Swiss Organic potato producers to control late blight with reduced amounts of copper (Musa-Steenblock and Forrer, 2005).

International Potato Centre has linked two disease forecasting models, Blitecast and Simcast to climate database in a geographical information system (GIS) to estimate global severity of potato late blight. Tropical highlands are the zone of high late blight severity. Major production zones with a low late blight severity include Western Plains of India, where irrigated potato is grown in the cool dry season, North Central China

and North- Western USA. Average number of sprays calculated for different countries using GIS database of potato production compared with estimated current fungicide use revealed that the estimated number of sprays in developing countries whether from Blitecast or Simcast, predicted optimum number of sprays much higher as compared with the actual number observed. On the basis of GIS database it was suggested that an increased access to host resistance and fungicides in developing countries could have a strong economic impact on potato production (Hijmans *et al*., 2000).

FORECASTING POTATO LATE BLIGHT: INDIAN EXPERIENCES

The work on late blight forecasting in India started in 1950's when Chaudhury and Pal (1959) utilized the rainfall data and dates of appearance of late blight in Darjeeling hills for 12 years using Cook's moving graph concept (Cook, 1949) and Hyre's concept (Hyre, 1954). They demonstrated that 7-day moving graph with critical rainfall line of 1.8" were more accurate than a 10-day moving graph for predicting the appearance of late blight in that area. Thus, criteria for late blight forecasting differed from region to region. Bhattacharyya *et al*. (1982) utilized daily weather data (temperature, rainfall and RH) and the date of actual appearance of late blight for Shimla, Shillong and Ootacamund. They established that if "7 day moving precipitation of at least 30 mm for Shimla, 28.9 mm for Ooty and 38.5 mm for Shillong hills with mean temperature of 23.9^0 C or less continue for 7 consecutive days, late blight would appear within 3 weeks". Once these conditions are met, then more accurate prediction based on RH and temperature was developed. It states that if hourly temperature remains in between $10\text{-}20^0$ C associated with the RH ≥80% for continuous 18 hr for at least 2 consecutive days, late blight would appear within a week. This model has been put to successful use for predicting late blight in Shimla hills since 1983 and it is still working very well. Similarly, late blight forecasting for eastern plains was also developed based on blight favourable days. The model specifies that first blight favourable period (BFP 1) of two consecutive days comprising of average minimum temperature (7-15°C), average maximum temperature (22-25°C; range 21.5-26±1°C), RH >75% and average sunshine < 5hr per day would predict late blight within 7-14 days of satisfying the conditions when the canopy is dense (crop age >35 days) and within 15-21 days when the crop canopy is sparse (crop age < 30 days) (Prasad and Singh, 2005).

Singh *et al*. (2000) used moving graph concept and developed a computerized forecasting model 'JHULSACAST' for western UP. Models for both rainy and non-rainy years were worked out. For rainy years, if i) measurable rains (0.1-0.5 mm) for a minimum of two consecutive days, ii) 5-day moving >85% RH period ≥50 hrs, and iii) 5-day moving congenial temperature ($7.2\text{-}26.6^0$ C) ≥105 hrs, blight would appear within 10 days. For non-rainy years, if 7-day moving >85% RH period is ≥60 hrs and 7-day moving congenial temperature period ($7.2\text{-}26.6^0$ C) is ≥120 hrs, blight would appear within 10 days. These models have been validated and are able to predict late blight accurately in western U. P. This JHULSACAST model is almost similar to BLITECAST developed by Krause *et al*. (1975) except that it is meant for forecasting the initial appearance of late blight. Besides, decision rules for predicting first appearance of late blight in Punjab under non-rainy conditions have also been developed recently using JHULSACAST model as template. The model specifies that 7-day moving sum of RH ≥85% for at least 90 hr coupled with a

7-day moving sum of temperature between 7.2-26.6°C for at least 115 hr would predict appearance of late blight within 10 days of satisfying the conditions (Arora *et al*., 2012). JHULSACAST has also been calibrated for Tarai Region of Uttarakhand (Pundhir *et al*., 2014) and the plains of West Bengal (Chakraborty *et al*., 2014).

Based on JHULSACAST, Decision Support System (DSS) has also been developed which has three components *i.e.* (i) prediction of first appearance of disease, (ii) decision rules for need based fungicide application, and (iii) yield loss assessment model. Fungicide spray is recommended on the day when the accumulated weighted congenial hours of severity is 150 and 175 for contact and systemic fungicides, respectively. The subsequent sprays are repeated after the accumulation of above severity values (CPRI, 2005). Besides, yield loss assessment model has been developed by utilizing 8 years severity data. With the help of curve fit software, linear and non-linear regression lines were developed. The deviation between actual observed yield loss and predicted yield loss ranged from 0 to 13.7% and the efficacy of the model was 84% (CPRI, 2012). Recently, JHULSACAST model was implemented in western Uttar Pradesh using Wireless Sensor Networks (WSN), which is web based, to forecast late blight and the model could forecast the disease well in advance in comparison to other forecasting models tested (Jagyasi *et al*., 2014).

MANAGEMENT

Reduction of the primary sources of inoculums is the first step in management of late blight. Control of contaminated sources such as waste heaps, infected tubers, volunteer plants, disease in neighbouring fields and re-growth after haulms destruction can help in management of the disease (Turkensteen and Mulder, 1999). It has been estimated that onset of epidemic can be delayed by 3 to 6 weeks if all primary infection from early potato can be eliminated. It has been shown that during most years late blight epidemics start from infected plants on dumps (Zwankhuizen *et al*., 2000), therefore, covering of dumps with black plastic sheet throughout the season and preventing seed tubers from becoming infected is an important step in reducing the primary inoculum (Cooke *et al*., 2011). The sheet must be kept in place and remain intact until the tubers are no longer viable. This will prevent re-growth and the proliferation of spores on the piles, reducing the risk to nearby crops. Oospores are a threatening primary inoculum source, especially with short crop rotation. Sandy and clay soils contaminated with oospores remained infectious for 48 and 34 months, respectively (Turkensteen *et al*., 2000). Use of early-maturing cultivars, pre-sprouting the seed and early planting can help to manage late blight. Avoiding excess nitrogen and use of moderate nitrogen fertilization is often recommended as a cultural practice to delay the development of late blight. Use of systemic fungicides early in the season is an effective strategy to manage late blight if source of primary infection is infected seed (Hermansen and Naerstad, 2009). Increased application of nitrogen can lead to increase in disease severity and use of more and more fungicides. Higher dose of phosphorus and potassium has been found to give a higher yield in a late blight year (Roy *et al*., 2001)

Importance of oospores as soil-borne inoculum is determined both by their formation in plant tissue and their survival in soil. There is a correlation between crop rotation and early blight infections. Infection usually starts early in fields which are not subjected to crop rotations. The decline in early infection was most pronounced in fields

subjected to crop rotations for three or more year between the potato crops (Bodker *et al*., 2006; Hannukkala *et al*., 2007). This indicated that a sound crop rotation is important and is an effective way of reducing the risk of soil-borne infections of *P. infestans*. Choice of suitable cultivars, well aerated fields, pre-sprouting of tubers, early planting and use of resistant varieties are some of the measures against foliar blight while planting potatoes on large steep ridges, right time of mechanical weeding and harvesting, avoiding rapid shift of harvested tubers or long transports could minimize tuber blight (Meinck and Kolbe, 1999).

Development of resistant cultivars and exploitation of screening methodology has played an important role in the management of late blight (Bhardwaj *et al*., 2005; 2007; Joseph *et al*., 2007; Kaushik *et al*., 2007; Joseph *et al*., 2011; Bhardwaj *et al*., 2013). *Solanum demissum*, a hexaploid wild species, has extensively been used to confer resistance against *P. infestans*. Field resistance is polygenic and more durable. *Solanum bulbocastanum*, *S. microdontum*, *S. verrucosum* and *S. chacoense* have been used as a source of field resistance in breeding programs. Since the pathogen is quite plastic and mutable matching races against major R genes develop readily in the pathogen and overcome the resistance of the new cultivars. However, major genes which have evolved naturally in *S. demissum* population for thousands of years where late blight occurs annually still hold their importance. A multilineal combination of resistant genes (R genes) identified so far, into commercial varieties has significant potential in management of late blight (Niederhauser *et al*., 1996). Molecular techniques have enabled the cloning, sequencing and generation of new transformants of commercial potato varieties. One such example is the transfer of resistance genes from *S. bulbocastanum* (diploid) to *S. tuberosum* (tetraploid) by protoplast fusion. Nucleic acid based studies have focussed in better characterization of the host for location and manipulation of resistance in specific chromosomes and genes of wild *Solanum* species, resulting in transgenic plants resistant to late blight (Lozoya-Saldana, 2011). Use of Marker assisted selection (MAS) is helpful in selecting genotypes at early selection stages without a pathogen inoculation test. Sharma *et al*. (2013) validated markers for resistance genes in indigenous and exotic potato genotypes and found genotypes (17) having combination of *R1*, *R2* and *R3a* genes which are now being utilised in Indian breeding programme for pyramiding these genes in a single host background. Somatic hybrids having high degree of resistance to late blight can be used as one of the parent for potato breeding (Tiwari *et al*., 2013). Demand for late blight resistant varieties is always at top priority of the farmers to manage the disease (Rana *et al*., 2011; 2013). Disease resistance in potato varieties together with use of fungicides can slow down the development of late blight. A variety with field resistance to late blight in tubers and a medium to high resistance in the foliage can help in reducing the use of fungicides.

Use of host density as a tool for management of late blight has been used for control late blight. Tuber yield from both resistant and susceptible cultivar increase when these were grown in mixture as compared to the single genotype stands (Garrett and Mundt, 2000). Strip cropping of potatoes significantly reduced late blight severity in organic production when the crop was planted perpendicular to the wind neighboured by grass clover (Bounes and Finckh, 2008).

Spraying with an effective fungicide has been a standard practice for control of late blight. Bordeaux mixture, which consists

of copper sulfate, hydrated lime and water was a standard fungicide for many years. Subsequently organic fungicides especially carbamates which controlled both early and late blight replaced Bordeaux mixture. Metalaxyl – a phenylamide group of fungicides specific to oomycetes however, revolutionized late blight control (Bruck *et al*., 1980). Since it was most effective its use increased rapidly and this became one of the major fungicide used world over but strains of *P. infestans* which do not respond to metalaxyl appeared worldwide (Dowley and O'Sullivan, 1981; Gisi and Cohen, 1996). Metalaxyl in mixture with unrelated contact fungicide however, could retard development of resistance in the pathogen. Cymoxanil mixtures have been found effective for managing metalaxyl resistant strains (Samoucha and Cohen, 1988). A synergism between cymoxanil and mancozeb has also been reported by Evenhuis *et al*. (1996). Fluazinam, cyazofamid and mandipropamid have also been used for the disease management. Spraying with effective fungicides (cyazofamid and mandipropamid) before periods with high risk of infections can give very effective control of late blight. Studies conducted in Denmark in 2009 showed that use of cyazofamid and mandipropamid could be reduced by 30% by adjusting the dose according to resistance level in a variety and used according to the infection pressure (Cooke *et al*., 2011). Application of sub-phytotoxic concentration of boron with reduced rate of fungicide propineb + iprovalicarb has been reported as more effective as compared to plants treated with fungicide alone (Frenkel *et al*., 2010).

Elexa, a plant booster which contains 4% chitosan, elicits specific defense responses and provided 60% protection against late blight (Acar *et al*., 2008). Spray mixtures consisting of plant activator BABA and the protectant fungicide mancozeb was more effective than BABA or mancozeb alone in controlling late blight. A mixture of 5 parts BABA and 1 part mancozeb (w/w, a.i.) exhibited a higher synergy factor than other combinations (Baider and Cohen, 2003). Foliar application of phosphonic acid substantially reduced infection of tubers by *P. infestans*. Healthy tubers of blight susceptible cultivars removed from treated plants and artificially inoculated did not develop symptoms demonstrating that phosphonate applications had directly reduced the susceptibility of tubers to infection, probably as a result of translocation into tuber tissue (Cook and Little, 2002). The neutralized phosphorous acid solution (1000mg/lt) completely inhibited the mycelial growth and sporangial germination of *P. infestans* and when applied as foliar spray to the potato plants 2-4 times at 7-day interval, the severity was significantly and effectively suppressed (Tsai *et al*., 2009). Similarly, Johnson (2008) also reported phosphorous acid as potential material for postharvest control of late blight and pink rot.

Heavy dependence on fungicides could pose threat to environment and human population (Bradshaw *et al*., 2000). Biocontrol agents and biopesticides could be a safe option to the use of synthetic fungicides. Antagonism to *P. infestans* by some naturally occurring microorganisms such as *Trichoderma viride*, *Penicillium virdicatum*, *P. aurantiogiseum, Chetomium brasilense* (CPRI, 1991; Gupta *et al*., 2004), *Acremonium strictum* (CPRI, 1999), *Myrothecium varrucaria*, *Penicillium aurantiogriseum* (Roy *et al*., 1991), *Epiccocum purpuranscens*, *Stachybotrys coccodes*, *Pseudomonas syringae*, *Fusarium graminearum* (Kim *et al*., 1995) and *Pythium ultimum* (Kuzuetsova *et al*., 1995) have been observed in laboratory and field studies. The antagonist *Bacillus subtilis* B5, when tested by dual culture, was found effective in

inhibiting the growth of *P. infestans* (Ajay and Sunaina, 2005). Lal *et al.* (2013) also reported the antagonistic activities of *Pseudomonas fluorescens, Pseudomonas* sp. *Aspergillus flavus, A. niger, Penicillium* sp., *Trichoderma virens* and *T. harzianum* against *P. infestans* under *in vitro* conditions. Biosurfactants can be used as alternatives to chemical surfactants as their capability of reducing surface and interfacial tension with low toxicity, high specificity and biodegradability make them important for inhibiting pathogens. The metabolite of biosurfactant producing microorganism (*Pseudomonas aeruginosa*) has shown high efficacy against *P. infestans* under *in vitro* conditions (Tomar *et al.*, 2013).The biocontrol agents in general have been found to be very effective under laboratory and glasshouse conditions but less effective under field conditions. However, an integrated use of biocontrol agents along with low dose of fungicides could help to reduce the quantity of fungicides used in the management of late blight (CPRI, 2001).

CONCLUSION

Late blight of potato is the most dreaded disease and will continue to remains as the pathogen is evolving at a fast rate and adapting to new environments and hosts. There is need to characterize the pathogen population with more robust molecular markers and to study the epidemiology of isolates grouped in different categories on the basis of markers. Disease resistant varieties should be developed keeping in view the changes in the pathogen population. Though different forecasting models have been developed across the world but none is universally applicable, hence this is the need of the hour to develop a forecasting model which is effective in most regions and seasons. As the pathogen has developed resistance to metalaxyl based fungicides, new molecules with different mode of action need to be identified and used along with compatible biocontrol agents to minimize the use of pesticides. As more and more information is being generated there is a need to develop an appropriate disease management strategy based on farmer friendly information technology.

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