Late Blight of Potato (Phytophthora infestans) Biology, Economic Importance and its Management Approaches

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Abstract

Late blight is the most destructive of all potato disease and responsible for the Irish Famine in the middle of the 19th century. It affects both potato foliage in the field and tuber in the storage which can absolutely destroy a crop, producing a 100% crop loss. The pathogen (*Phyhtophthora infestans*) have different mechanisms of survival and two infection phases in its life cycle. It requires two mating types, A1 and A2 to produce a sexual spore known as oospore. The spores are carried by wind and rain splash to healthy plants. A number of management techniques of late blight have been developed and used though out the world. Effective control of this disease requires implementing an integrated disease management approach. The most important measures are cultural control, use of resistant varieties, chemical control and integrated disease management. Integration of late blight management has often been thought as one of the better disease management options in tropical regions where fungal inocula are abundant in most months of the year.

Keywords: Irish Famine; Pathogen; Integrated Disease Management (IDM); Life cycle

INTRODUCTION

Late blight of potato, which is caused by *Phytophthora infestans* (Mont) de Bary is the major bottleneck in potato production in Ethiopia (Bekele and Yaynu 1996) and other parts of the world (Fry and Goodwin 1997b). It is the best known, highly studied and still the most destructive of all potato disease (Jones 1998). Late blight is probably the single most important disease of potatoes and tomatoes worldwide (Son et al. 2008). Worldwide losses due to late blight are estimated to exceed \$5 billion annually and thus the pathogen is regarded as a threat to global food security (Latijnhouwers et al. 2004). Late blight was responsible for the Irish potato famine in the 1840s (Mercure 1998). The disease caused yield losses ranging from 31-100% in Ethiopia depending on the variety used (HARC 2007). Cultural control measures such as eliminating cull piles and volunteer potatoes, using proper harvesting and storage practices, can be used to reduce the pathogen populations by reducing its survival, dispersal and reproduction (Garrett and Dendy 2001). Use of fungicides like metalaxyl in controlling the disease was found to boost potato yield in various East African countries (Nsemwa et al. 1992; Rees et al. 1992). Potato late blight management strategies have changed considerably following the migration of metalaxyl resistant isolates of P. infestans from Mexico to North America (Fry and Goodwin 1997b) and necessitated utilization of cultural control measures and modification of the previous chemical control practices. Potato late blight is probably the most studied plant disease in the world; yet relatively fewer alternative management options other than synthetic chemical fungicides are available. At a global level, the major approach to prevent late blight development has been through application of fungicides (CIP 1989). But highly aggressive strains of this disease many insensitive to popular synthetic fungicides, have surfaced and created new challenges for potato and tomato producers (Powelson and Ingils 1998).

The use of protectant and systemic fungicides for managing late blight has perhaps been the most studied aspect of late blight management in the temperate countries (Olanya et al. 2001). In tropical Africa, however, fungicide application intervals, frequency of application and timing, and fungicide dose response relationships have not been well investigated (Kankwatsa et al. 2002). Excellent control of the late blight disease was achieved through the use of the phenyl amide fungicides, like Ridomil across the Sub-Saharan Region (Dekker 1984; Fekede et al. 2013; Binyam et al. 2014a). According to Mesfin and Gebremedhin (2007), the failure of Ridomil in giving perfect control of the disease in some countries of the Sub-Saharan Region and in some cases the intensive frequency of usage (Davidse et al. 1981; Schiessendoppler et al. 2003), leads to the development of an integrated disease management strategy involving resistant and susceptible varieties and fungicide sprays. The best management of late blight and high marginal rate of return was obtained on plots treated with combinations of all tested potato varieties and 0.75 kg ha⁻¹ Ridomil application followed by 1.5 kg ha⁻¹ Ridomil application (Binyam et al. 2014b). Fontem and Aighew (1993) reported that, application of fungicides for late blight management increases potato tuber yield by as much as 60%. As we know it is the most studied and well known disease of potato in this world. In addition there are so many important research works which are done about this disease all over the world. However, these research results are not compiled in well structured review paper. With this perspective this paper is initiated to review on late blight of potato's biology, economic importance and its management approaches.

GEOGRAPHICAL DISTRIBUTION AND ECONOMIC IMPORTANCE OF LATE BLIGHT

Late blight is one of the most popular, most studied and most serious disease of potato in many regions of the world (Erwin and Ribeiro 1996). During the last two decades, this disease has increased globally (Fry and Goodwin 1997a). It occurs almost everywhere potato is grown (Paul 1992). Potato late blight is considered to be the most serious potato disease worldwide (Agrios 2005). It is a very serious economic threat in the vast majority of potato production systems, as well as many tomato production systems worldwide (Madden 1983). It is one of the few plant diseases that can absolutely destroy a crop, producing a 100% crop loss (Mercure 1998). The potential economic and social impact of this disease is best illustrated by the well-publicized role it played in the Irish Famine in the middle of the 19th century when it destroyed a large portion of the potato crop, either by eliminating foliage prior to the harvest or by causing massive tuber rot in storage. As a result of the famine, millions of Irish died or emigrated (Bourke 1993). Late blight may cause total destruction of all plants in a field within a week or two when weather is cool and wet (Hooker 1981; Fry *et al.* 1993; Van der Zaag 1996; Agrios 2005). The disease is also very distractive to tomatoes and some other members of the family solanaceae. Late blight may kill the foliage and stems of potato and tomato plants at any time during the growing season. It also attacks potato tubers and tomato fruits in the field, which rot either in the field or while in storage (Agrios 2005). It attacks the leaves, stems, and tubers of potato plants (Mercure 1998).

The average global crop losses of all diseases combined was approximately 12.8% of the potential production but potato alone was subjected to 21.8% loss (James 1981). In Ethiopia the disease caused 100% crop loss on unimproved local cultivar, and 67.1% on a susceptible variety (Bekele and Yaynu 1996). Late blight is a major limitation to potato production in high humid elevations; with estimate average yield losses of about 30–75% on susceptible varieties (Olanya *et al.* 2001). Research centers have made estimates of losses ranging from 6.5 to 61.7%, depending on the level of susceptibility of the varieties (GILB and CIP 2004a). According to Fekede *et al.* (2013); Binyam *et al.* (2014b), reports, in Ethiopia late blight of potato causes tuber yield losses of 21.71–45.8% and 29-57% depending on the resistance level of the cultivars, respectively. Late blight can occur at any time during the growing season, it is more likely to be seen in late summer and early autumn (Bevacqua 2000). In the temperate regions of North America, potato late blight has caused tremendous economic impact over many years due to potato crop loss or destruction (Guenthner *et al.* 2001).

Late blight has probably spread worldwide through its association with potato internationally traded seed (Fry *et al.* 1993). It is the most devastating disease of potato in countries like Ethiopia where subsistence farmers do not know the cause, epidemiology and control of the disease. In Ethiopia the disease occurs throughout the major potato production areas (GILB and CIP 2004a). In spite of the obvious destructive potential of late blight, it is extremely difficult to measure losses due to this disease because other factors simultaneously affect the tuber yield (Madden 1983). In a national assessment, the economic impact of potato late blight in all of the USA was estimated to be about 210 million US Dollar (Guenther *et al.* 2001). The CIP has made a global estimate of late blight damage in developing countries based on an average production loss of 15%. This translates into a total production loss in developing countries of approximately 2.75 billion US Dollar. One important way of viewing the economic effects of potato late blight is by assessing fungicide usage, which is easier to estimate the fungicide cost than crop loss. Based on this, CIP estimated fungicide use in developing countries at 750 million US Dollar. Based on these estimates, about 1 billion US Dollar per year is spent on fungicides to control late blight in the US, Europe and developing countries (Anonymous 1997 as cited by GILB and CIP 2004b).

THE PATHOGEN

The causal organism of potato late blight is *Phytophthora infestans* (Mont.) de Bary (Jones 1998). The genus *Phytophthora*, belongs to the Oomycetes, which are unrelated to true fungi (Shaw and Khaki 1971). The genus *Phytophthora* contains some species (including *P. infestans*) that are heterothallic (A1 and A2 mating types) (Fry *et al.* 1993). The mycelium produces branched sporangiophores that produce lemon-shaped sporangia at their tips. At the places where sporangia are produced; the sporangiophores form swellings that are characteristic for this fungi (Agrios 2005). *P. infestans* is the best known, most studied and still among the destructive of all potato diseases of the species of phytophthora (Jones 1998). Recent studies of Ethiopian isolates found all those tested to date to be A1 mating-type and the Ia mt-DNA-haplotype (GILB and CIP, 2004a). In Ethiopia during year of 1982 and 1983 cropping seasons, different races of the pathogen were detected at Ambo SPL, Holetta, Debre Zeit and Bako. These races are: 4; 8; 10; and 11, and 2.4; 1.3; 3.4 and 14, respectively. The R-gene resistance of these races of the pathogen may not be very useful in reducing incidence of the disease but may be responsible for increasing pathogenic variety (Tsedeke 1985).

P. infestans requires two mating types, A1 and A2, to come into contact to produce a sexual spore known as an oospore (Kirk 2009). Until the late 1980s, only one mating type was present in countries outside Mexico. Since then, however, both mating types have become widely distributed in most countries and, as a result, new strains

of the pathogen have appeared. Some of the new strains are much more aggressive than the old ones and quickly replace them. When the two mating types grow adjacently, the female hypha grows through the young antheridium (male reproductive cell) and develops into a globose oogonium (female reproductive cell) above the antheridium. The antheridium then fertilizes the oogonium, which develops into a thick-walled and hardy oospore. Oospores germinate by means of a germ tube that produces a sporangium, although at times the germ tube grows directly into the mycelium. Sporangia germinate almost entirely by releasing three to eight zoospores at temperatures up to 12 or 15 °C, whereas above 15 °C sporangia may germinate directly by producing a germ tube (Agrios 2005).

DEVELOPMENT, EPIDEMIOLOGY AND LIFE CYCLE OF LATE BLIGHT

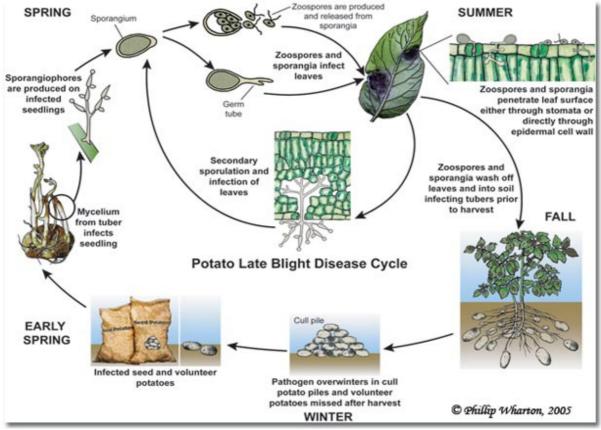
At temperatures of 13-21 °C, sporangia germinate by means of a single germ tube. Night temperatures of 10-16 °C accompanied by light rain, fog or heavy dew and followed by days of 16-13 °C with high relative humidity are ideal for late blight infection and development (Kirk 2009; Kirk et al. 2013). Temperatures above 30 °C slow or stop the growth of the fungus in the field but do not kill it, and the fungus can start to sporulate again when the temperature becomes favorable, provided, of course, that the relative humidity (near 100%) is sufficiently high (Agrios 2005). The first symptoms of late blight in the field are small, light-to-dark green, and circular-to irregularly-shaped, water-soaked lesions (Kirk et al. 2013). These usually first appear on the lower leaves where the microclimate is more humid (Martin et al. 1994). However, they may occur on upper leaves if weather conditions are favorable and the pathogen has been carried into the field by air currents (Martin et al. 1994; Kirk et al. 2013). In moist weather the lesions enlarge rapidly and form brown, blighted areas with indefinite borders. A zone of white, downy mildewy growth 3-5 mm wide appears at the border of the lesions on the undersides of the leaves. Soon entire leaves are infected, die, and become limp (Agrios 2005). Conditions must remain moist for a minimum of 7-10 hours for spore production to occur (Martin et al. 1994). Because of this relationship, spores or lesions are most apparent after wet nights or periods of rainfall. The fungus may appear as a white, mildew-like growth at the edge of the lesion, primarily on the underside of the leaf. It is this white growth that distinguishes late blight from several other foliar diseases of potatoes. The spores are carried by wind and rain to healthy plants where the disease cycle begins again. The development of late blight epidemics depends greatly on the prevailing humidity and temperature during the different stages of the life cycle of the fungus. The fungus can complete many reproductive cycles in a season, accounting for the rapid increase of disease once it becomes established in a field. When conditions are continuously wet all tender aboveground parts of the plants become blight and rot away giving off a characteristic odor. Entire potato plants and plants in entire fields may become blighted and die in a few days or a few weeks. In dry weather the activities of the pathogen are slowed or stopped. Existing lesions stop enlarging, turn black, curl, and wither, and no oomycete appears on the underside of the leaves. When the weather becomes moist again the oomycete resumes its activities and the disease once again develops rapidly (Agrios 2005).

Tubers may be infected by P. infestans whenever sporangia and tubers come into contact, from early in the tuberization process until harvest. Infections most commonly occur when sporangia are washed from lesions on stems and foliage to the soil and then through the soil to tubers. Infections can occur on developing or mature tubers, but contact between tubers and sporangia is more likely when the tubers are enlarging; tuber enlargement creates cracks in the soil and gives sporangia ready access. Tubers become infected most often when soils are cool and wet (near field capacity); soil temperatures higher than 18 °C seem to suppress infections. Because sporangia can survive days or weeks in soil, tubers can become infected for a period of time after infections in the foliage are no longer producing sporangia (Fry 1998). The affected tubers at first showed more or less irregular purplish-black or brownish blotches, when cut open the affected tissue appears water-soaked, dark, somewhat reddish brown, and extends 5-15 mm into the flesh of the tuber. Later the affected areas become firm and dry and somewhat sunken. Such lesions may be small or may involve almost the entire surface of the tuber without spreading deeper into the tuber. The rot, however, continues to develop after the tubers are harvested. Infected tubers may be subsequently covered with sporangiophores and spores of the pathogen, or infected tubers may be subsequently invaded by secondary fungi and bacteria, causing soft rots and giving the rotting potatoes a putrid, offensive Oder (Agrios 2005). The extent of rotting in a tuber depends on the susceptibility of the cultivar, temperature, and length of time after the initial infection (Martin et al. 1994; Kirk et al. 2013).

Phyhtophthora infestans can survive in living host tissue, such as in seed tubers, cull piles, and volunteer potatoes that over-winter in the field (Shinners *et al.* 2003), on other solanaceous plants and in the soil (Kirk *et al.* 2013). It usually survives from year to year in infected tubers placed in storage, in piles of cull potatoes or in infected tubers missed during harvest that remain unfrozen over the winter (volunteer potatoes). In the spring, the pathogen can be transmitted from infected tubers in cull piles or volunteers to potato foliage by airborne spores. Infected seed-potatoes are also important sources of the disease. Some infected tubers may rot in the soil

before emergence, and not every plant that emerges from an infected tuber will contract late blight. Sporangia of *P. infestans* may be spread from infected plants in one field to healthy plants in surrounding fields by wind, splashed rain, mechanical transport and animals (Martin *et al.* 1994; Kirk 2009; Kirk *et al.* 2013; Figure 1). A fewer days after infection, new sporangiospores emerge through the stomata of the leaves and produce numerous sporangia, which are spread by the wind and infect new plants. In favorable weather, the period from infection to sporangia formation may be as short as 4 days and, therefore, a large number of asexual generations and new infections may be produced in one growing season. The sporangia, when ripe, become detached and are carried off by the wind or are dispersed by rain; if they land on wet potato leaves or stems, they germinate and cause new infections (Agrios 2005).

Sporangia of *P. infestans* germinate either directly with a germ tube or indirectly, by liberating zoospores. Germ tubes can also form secondary sporangia, which may serve to increase the longevity of the spore (Harrison 1992). Sporangia may germinate at temperatures between 7 and 13 °C when free water is present on leaves and form 8-12 motile zoospores per sporangium. These swim freely in water films, attach to the leaf surface and infect the plant. Encysted zoospores infect leaves by penetrating the leaf surface with a germ tube, either through stomata or by means of direct penetration (Kirk 2009; Kirk *et al.* 2013). The germ tube penetrates directly or enters through a stomata, and the mycelium grows profusely between the cells, sending long, curled haustoria into the cells. Older infected cells die while the mycelium continues to spread into fresh tissue. In any case, as the disease develops, established lesions enlarge and new ones develop, often killing the foliage and reducing potato tuber yields (Agrios 2005; Figure 1.).



Figure, 2. The life cycle of the late blight pathogen *Phythophtora infestans* (Wharton 2005).

The second phase of the disease begins in the field during wet weather, when sporangia are washed down from the leaves and are carried into the soil. Emerging zoospores germinate and penetrate the tubers through lenticels or through wounds. In the tuber the mycelium grows mostly between the cells and sends haustoria into the cells. Tubers contaminated at harvest with living sporangia present on the soil or on diseased foliage may also become infected. However most of the blighted tubers rot in the ground or during storage. The fungus grows and sporulates most abundantly at a relative humidity near 100% and at temperatures between 15 and 25 °C (Agrios 2005).

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SUSTAINABLE LATE BLIGHT MANAGEMENT APPROACHES

A number of management techniques of late blight have been developed and used. Effective control of this disease requires implementing an integrated disease management approach. The most important measures are cultural, use of resistant cultivars and chemical controls.

CULTURAL CONTROL

There are different methods of cultural practices applicable for late blight management. Cultural practices are the first line of defense against late blight (Kirk 2009; Kirk *et al.* 2013). Cultural practices can be applied to reduce the pathogen population; by reducing its survival, reproduction, dispersal and penetration of the pathogen. Survival of *P. infestans* to initiate epidemic can be reduced through avoidance of introducing late blight into a field by planting only disease-free seed tubers, preferably certified seed, destroying all cull and volunteer potatoes, avoid frequent or night-time overhead irrigation and good soil coverage (Draper *et al.* 1994). Late blight is controlled by eliminating cull piles and volunteer potatoes, using proper harvesting and storage practices, and applying fungicides when necessary (Davis *et al.* 2009). The most effective strategy for managing late blight is to avoid sources of inoculum. The initial sources of inoculum are likely to be infected potatoes in cull piles, infected volunteer potato plants that have survived the winter, and infected seed tubers. Therefore, it is important to keep a clean operation by destroying all cull and volunteer potatoes (Agrios 2005). Seed sources should be selected carefully to avoid bringing in late blight on seed, especially new strains of the pathogen (Kirk 2009). When partially blighted leaves and stems are surviving at harvest time, it is necessary to remove the aboveground parts of potato plants or destroy them by chemical sprays (herbicides) or mechanical means to prevent the tubers from becoming infected (Agrios 2005).

The cultural measures include: the use of disease free/healthy seed, removal of volunteer potato plants, hilling with adequate amounts of soil and management of plant nutrition (Garrett and Dendy 2001). Avoiding conditions that favor late blight development is very important in managing the disease. Weather conditions strongly influence the incidence and severity of late blight. Although weather conditions are beyond many control, field selection and carefully managed irrigation practices can help reduce the extent of periods favorable for disease development. Fields with good water infiltration and drainage characteristics are desirable for planting potatoes. After planting and early in the season, it is important to get rid of cull potatoes and potato pieces resulting from seed cutting operations or left after loading or unloading at storage facilities as these may support the production of inoculum whether or not the pieces are sprouting. It is also beneficial to control weeds and alternative late blight hosts such as hairy nightshade (solanaceae) family, which may contribute to disease spread under some conditions. Although weed species are not late blight hosts, they can contribute to conditions that favor disease development by restricting air movement within the canopy. Heavy weed infestations also prevent adequate coverage of potato foliage with fungicides (Kirk 2009; Kirk *et al.* 2013).

Since wet conditions are favorable for infection, sprinkler irrigation should be carefully scheduled, or minimized, particularly late in the season when the closed potato canopy provides ideal conditions for late blight development. If possible, rows should be oriented parallel with prevailing winds to encourage better air circulation and foliage drying. Studies in Israel noted that late blight infection was greater on morning-irrigated potatoes than on potatoes irrigated at midday or evening (Carlson 1994). Late season excessive irrigation and fertilizer applications should be limited. Vines should also be killed at least two weeks before harvest. It may also be beneficial to spray foliage after vine killing with labeled fungicides to kill living late blight spores on the foliage (Kirk *et al.* 2013). Harvest should be dry when placed in storage, and the storage air temperature and humidity should be managed (Kirk 2009). Store tubers harvested from diseased fields, separately from that of healthy fields. Potatoes should be stored dry and at the lowest temperature possible to suppress pathogen growth and spread. Scouting all stored potatoes frequently and removing diseased tubers from storage is desirable to prevent disease spread (Stone 2009).

HOST-PLANT RESISTANCE

Host resistance to late blight is of significance in integrated late blight management due to its long-term economic benefits for farmers. It also minimizes changes in the population structure of *P. infestans*, decreasing the likelihood of fungicide resistance (Hakiza 1999; Mukalazi *et al.* 2001). The use of resistant varieties is among the most effective and environmentally safe means of managing the disease. Thus, breeding for resistance to *P. infestans* started in the 19th Century and has continued at a slower rate. Variations in resistance to late blight among different potato varieties have been demonstrated by several researchers (Njualem *et al.* 2001). Biotechnology is also being employed in the pursuit of late blight resistance. Genetically-engineered plants, however, are not acceptable for organic production (Shapiro *et al.* 1998). But, potato cultivars with high blight

resistance can be destroyed by new strains of the fungus since the resistance is controlled by single gene. Some varieties have a low level of resistance which can give some protection in drier seasons but offer little advantage. Blight can be controlled in partially resistant varieties governed by minor genes combined with reduced dose of fungicide. Cultivars having high levels of resistance, can allow them to be grown without chemical protection even in the wettest growing seasons. Most resistant varieties have main crop maturity. Early-maturing varieties are usually susceptible to the disease with exception of some cultivars. Some varieties have useful foliage resistance but poor tuber-blight resistance. Yet, others have good tuber-blight resistance but poor foliage-blight resistance. Ideally, a variety should have good resistance to both foliage and tuber blight (Anonymous 2007).

The use of durable or polygenic resistance is sometimes interpreted to be synonymous with intermediate resistance levels but cultivars ranging from complete susceptibility to very high resistance. Polygenic resistance has proved to be helpful in reducing the amount of fungicides (Jones 1998). Cultivars with polygenic resistance have significantly reduced area under disease progress curve (AUDPC) values compared with susceptible ones (Fry 1977). The use of plants with field resistance can also slow the pathogen growth rates. There is a diversity among commercial potato cultivars in terms of resistance to late blight and these levels can be incorporated into an overall management strategy (Jones 1998). However, no potato varieties are fully resistant to late blight (ATTRA 2004). Most resistant varieties are not immune to late blight but possess varying degrees of resistance to various races of the pathogen (Popokova 1972). Cultivars with higher level of resistance require less fungicide spray than cultivars with lower levels of resistance (Fry 1978). There are some released improved varieties that have lost their resistance to late blight, but still some are best in tolerating late blight when supported by reduced dose and rates of fungicide application (GILB and CIP 2004a).

Use of resistant varieties is one of the main components of late blight management and is especially effective under tropical conditions (Shtienberg *et al.* 1994). However, the race-specific oligogenic resistance (CIP 1989) in the existing released potato varieties can be rapidly broken down by compatible races of *P. infestans* rendering the varieties to be susceptible to the disease within a short period (Shtienberg *et al.* 1994). Generally resistant potato varieties and improved cultural practices can reduce late blight (FAO 2008). It is not sufficient to rely on varietal resistance to control late blight, as, in favorable weather, late blight can severely affect these varieties unless they are sprayed with a good protective fungicide. Even resistant varieties should be sprayed regularly with fungicides to eliminate, as much as possible, the possibility of becoming suddenly attacked by races of the fungs to which they are not resistant. However, it is always advisable to use resistant varieties, even when sprays with fungicides are considered the main control strategy, because resistant varieties delay the onset of the disease or reduce its rate of development so that fewer sprays on a resistant variety may be needed to obtain a satisfactory level of control of the disease (Agrios 2005). According to Binyam *et al.* (2014a), onset of the potato late blight disease was delayed almost by 20 days on the moderately resistant varieties as compared to the moderately susceptible and susceptible varieties.

CHEMICAL CONTROL

At a global level, the major approach to prevent late blight development has been application of fungicides (CIP 1989). Unlike insecticides and some herbicides that kill established insects or weeds, fungicides are most commonly applied to protect healthy plants from infection by plant pathogens. Protection by fungicides is temporary because they are subject to weathering and breakdown over time. They also must be reapplied at certain intervals to protect new growth when disease threatens (Lyr 1995). Fungicides that are used against late blight can be classified into two basic mobility groups: protectant or penetrant. Fungicides can slow or stop the development of new symptoms if applied in a timely fashion, but fungicides will not cure existing light blight symptoms (Beckerman 2008). Hence, most fungicides need to be applied before disease occurs or at the first appearance of symptoms to be effective. Also, the damage caused by late blight on plants often does not go away, even if the pathogen is killed. Fungicides can only protect new uninfected growth from the disease. Generally, few fungicides are effective against pathogens after they have infected a plant (McGrath 2004). Several broad-spectrum and systemic fungicides are used against potato late blight control. The new strains of the oomycete produced as recombinants of fertilization of the two mating-types (A1 and A2) are resistant to some of the systemic fungicides like, metalaxyl and, therefore, sprays with such materials are ineffective against such strains. Protective spraying of foliage usually affects a considerable reduction in tuber infection. Experimental, but not yet practical control of the disease, has been obtained by the pretreatment of tomato plants with the chemical dl-3-amino-butyric acid or pre-inoculation with tobacco necrosis virus, both of which induce systemic-acquired resistance (SAR) in the tomatoes, protecting them from late blight infection. Haustoria formation and growth of hyphae in SAR induced leaves against P. infestans appear inhibited, different, and damaged. Certain pathogenesis-related proteins accumulate in the leaves of treated plants and only in plant wall papillae and in the cell walls of the oomycete pathogen (Agrios 2005). Up to 80, 76, 75.5, 69 and 68% severity reduction was obtained from the varieties Bedassa, Gabissa, Chiro, Harchassa and Zemen plots treated with Ridomil at 3 kg ha⁻¹ rate of application, respectively (Binyam *et al.* 2014a).

The use of fungicides in controlling late blight was found to boost potato yield in Ethiopia (Nsemwa et al. 1992; Rees et al. 1992; Mesfin and Gebremedhin 2007). In Ethiopia the first spray with Ridomil MZ 63.5% WP at a rate of 2 kg ha⁻¹ followed by 2-3 sprays (need base application) of Dithane M-45 (mancozeb) at a rate of 3 kg ha⁻¹ ¹ were found to be effective in controlling late blight. When applying fungicides, complete coverage of the foliage (stems and leaves, top to bottom of canopy) with fungicide is necessary to enable disease prevention, regardless of the application methods (ground or air, traditional or newer technology sprays) (MAFRI 2002). Despite the fact that fungicide use increases production costs and has negative consequences on environment and human health, the efficacy of fungicides is appealing to resource-poor farmers and fungicide use is a common practice in almost all developing countries (Forbes et al. Undated). According to McGrath (2004), effective control necessitates multiple applications of fungicides, sometimes as frequently as every 5 days for many diseases. Repeated applications are needed to protect new growth and to replace fungicide lost from the plant by chemical decomposition, UV-light degradation, and erosion by wind and rain water wash. Modern approaches in chemical control emphasizes on reducing fungicide inputs, combined with using potato cultivars possessing acceptable levels of non-race specific resistance to late blight (Fry 1975, 1977; Clayton and Shattock 1995; Lambert and Currier 1997; Secor and Gudmestad 1999; Kirk et al. 2001). The disease is primarily controlled by use of resistant cultivars and fungicide sprays (Namanda et al. 2004). However, concerns about the environment, public health, and fungicide resistance have stimulated efforts to reduce the amount of fungicide used in late blight management (Shtienberg et al. 1994). In Ethiopia, farmers frequently apply fungicides to control late blight but the economic benefit accruing from the fungicide spray have not been established (Bekele and Hailu 2001). Binyam et al. (2014a) also reported that, reduced rates of Ridomil application resulted in better management of potato late blight with the highest marginal rate of return.

INTEGRATED DISEASE MANAGEMENT (IDM)

Integrated pest management has helped farmers drastically reduce the need for chemical controls while increasing production (FAO, 2008). Effective control of late blight requires implementing an integrated disease management approach (Martin et al. 1994; Kirk 2009; Kirk et al. 2013). Integration of different management options, including cultural practices (good crop husbandry), resistant varieties and fungicides is required to control late blight. Late blight of potatoes can be controlled successfully by a combination of sanitary measures, resistant varieties, and well-timed or scheduled chemical sprays (Agrios 2005). In integrated management of disease the host resistance contributes to reducing the number of sprays required to keep late blight below an economic threshold level (Jones 1998). Integration of late blight management has often been thought as one of the better disease management options in tropical regions where fungal inocula are abundant in most months of the year (Olanya et al. 2004). These include: variation of frequency of application based on host resistance of potato varieties (reduced fungicide use), early planting and improved variety (early and mid-maturity, tolerant variety (Kankwatsa et al. 2002). In potatoes current control practices require spraying every 5 to 10 days after the vines reach 15-30 cm if disease spread is indicated by predictive programs such as BLITECAST. Other control measures include: use of disease-free seed; eliminating cull piles; planting resistant cultivars; and killing potato foliage 10 to 14 days before harvesting. Killing foliage prevents migration of disease from foliage to tubers (Thornton and Sieczka 1980). The integration of reduced rate of Ridomil application and moderately resistant potato varieties, in the management of potato late blight is very important in reducing environmental pollution and input cost of the fungicide, and increase in production and profitability of high quality potato tuber yield (Binyam et al. 2014a).

For effective control of late blight, integrated management must be adopted by all producers, including large and small-scale farmers. Fungicides cannot be used alone for effective control of late blight, but must be used as one tool in an integrated management strategy. Cultural practices are the first line of defense, and forecasting techniques and proper application technology are essential for efficient, targeted applications of fungicides (MAFRI 2002). The integration (combination) of moderately resistant varieties and reduced rate of Ridomil application were resulted in lowering incidence of late blight of potato at 59 days after planting of disease assessment (Binyam *et al.* 2014a). In Ethiopia for the past 10 years integrated disease management of late blight (IDM-LB) has been adopted as a strategy. Integrated disease management of late blight includes host resistance in combination with cultural practices such as early planting dates and reduced dose and rate of fungicide use. Experimental plots with IDM-LB yielded 50% and 75% more than late planting (planting during the month recommended for potato-growing) alone (GILB and CIP 2004a). According to Binyam *et al.* (2014a), cost effective management of late blight was obtained by integrating potato varieties with the lowest rate of Ridomil application. The combinations of the varieties Gabissa, Chiro, Harchassa, Bedassa and Zemen with 0.75

kg ha⁻¹ Ridomil application were resulted in up to 28, 21, 18, 16 and 13% marginal rate of returns, respectively (Binyam *et al.* 2014b).

CONCLUSION

Since potato is considered as highly recommended food security crop that can help shield low-income countries from the risks posed by rising international food prices, identifying its major production constraint is very important. Among its production constraints late blight is the most destructive and can cause a total crop loss. Therefore understanding its development, epidemiology and life cycle are most important in selecting and implementing its effective management strategy. There are different types of management options of potato late blight, which can help in reducing its effect. But because of its new strain development, there is no single effective management strategy of late blight of potato in this world. Therefore, adopting integrated disease management (IDM) approach is the most effective, environmentally safe (to both humans and animals), and low costly to the users.

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