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STATUS AND MANAGEMENT OPTIONS OF *PHYTOPHTHORA INFESTANS, A CAUSAL AGENT OF THE* LATE BLIGHT DISEASE OF TOMATO, IN TROPICAL AFRICA

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ABSTRACT

Late blight disease caused by *Phytophthora infestans* (Mont.) de Bary is a serious challenge in tomato (*Solanum lycopersicum* L or *Lycopersicon esculentum* L) production worldwide. In tropical Africa, the disease is increasing always due to its biology and different complex infection mechanism(s) used by its causative pathogen to survive, spread, and invade the tomato host plant and environment. Management options of the disease, such as integrated disease management (IPM), use of resistant tomato varieties, use of plant extracts and synthetic chemical pesticides have been recommended but are either poorly practised or limited in tropical Africa. Thus, this review discusses the status and commonly recommended management options against late blight disease-causing pathogen(s) including the pathogen strain complexes so that tomato growers and other stakeholders can understand specific strains and how they can design appropriate managerial approaches to halt challenges of the disease in tomato production in the tropical Africa.

Key words: Host range, Pathogen infection Mechanism, Sign and Symptoms and Plant extract.

INTRODUCTION

Tomato (*Solanum lycopersicum* L. or *Lycopersicon esculentum* L.) is one of major vegetable crops grown for both nutritional and economical values worldwide (Wachira *et al.*, 2014). Nutritionally, tomatoes are a major source of lycopene a powerful antioxidant, vitamins C, beta-carotene (vitamin A), biotin (Vitamin B), vitamin K, vitamin B6 (Pyridoxine), niacin (vitamin B3), vitamin E and mineral nutrients mainly potassium, copper, manganese and phosphorus(Bhowmik *et al.*, 2012).

Despite its economic importance, tomato is susceptible to a wide range of diseases, such as bacterial wilt (*Ralstonia solanacearum*) (Aloyce *et al.*, 2017), verticillium wilt (*Verticillium dahliae*), early blight (*Altanaria solanii*), and late blight (*Phytophthora infestans*) among others (Kamoun, 2007). Of these diseases, the late blight disease caused by *Phytophthora infestans* (*P. infestans)*(Mont.) de Bary is the most significant and economically important disease causing over 50% loss in the tropical Africa (Fontem *et al.*, 2005). The late blight-causing pathogen also causes massive destruction in others crops in the solanacea family such as potato, eggplant, pear melon and tree tomato (Agrios, 2005; Nowicki *et al.*, 2013).

The late blight disease causes loses in terms of reduced crop yield, poor quality of fruits and diminished storability (Nowicki *et al.*, 2012). The late blight disease-causing-pathogen is seriously deadly to tomato due to its biology, wide host range and difficulties in managing it. This article, therefore, reviews the status, biology of the tomato late blight pathogen, its host range, and management options under African tropical climatic conditions. The information that is discussed here will be vital for accurate understanding of the causes, host range and how the pathogen can be managed within the tropical African context.

Status of tomato late blight disease in tropical Africa: In the tropical Africa, late blight disease is constantly re-emerging in every growing season and where it occurs, it spreads very rapidly within the leaves and fruits of the infected plants in the field, and consequently, spreading out to the entire field causing economic loss and often total destruction of the crops in the field (Agrios, 2005). Furthermore, the pathogen has ability to reproduce both asexually and sexually (Fig 1.) and has different kinds of strains which allow faster development in the field (Nowicki *et al.*, 2012). The sexual and asexual life cycles make the infection by *P. infestans* on tomato and other hosts to be very successful in the tropical environments (Nowicki *et al.*, 2012). The asexual form of the *P. infestans* serves as a major vehicle driving epidemics during the growing seasons whereas the sexual form proliferate during the off-seasons (Foolad *et al.*, 2008). After attack, the pathogen kills the leaves, stems and fruits of the affected host plant (Agrios, 2005).

Disease management involving cultural, biological and chemical control have been recommended but the disease is still challenging due to re-emergence of *P. infestans* with its enhanced ability to develop more virulent isolates through sexual recombination (Agrios, 2005). Chemical control which include synthetic fungicides such as metalaxyl spray are among the most widely used methods, however, they are ineffective to new strains of the oomycete produced as recombinants of fertilization (Axel *et al*., 2012). The fungicides are also costly to be afforded by most poor farmers, are challenged by development of resistance by the different *P. infestans* strains, and they have detrimental effects to human health and the environment. In addition, variation in pathogen strains (Table 1) further complicates not only management options but also how to correctly identify them. Therefore, there is a need to use improved methods such as Polymerase Chain Reaction (PCR) for accurate identification of pathogen strains involved in order to design strain-specific management options for tropical Africa.

Biology of *P. infestans*

Pathogen description: The name *Phytophthora infestans* literally means, "Plant destroyer". It is a fungus-like organism classified under Oomycetes in the kingdom Chromista and order Peronosporales (Nelson, 2001). It causes late blight disease in solanaceae plants especially during cool and moist period worldwide (Fry *et al*., 2013). There are many different types of pathogen strains that genetically vary between their virulence and mating types (Table 1) (Kamoun *et al*., 2015).

The pathogen is commonly described as coenocytic oomycete with rare cross walls (Kamoun *et al*., 2015). Sporangia are 29-36 x 19-22 µm and are ellipsoid to lemon shaped with a small pedicel. In culture, the pathogen mycelium is white and fluffy (Rumpf *et al*., 2010). The primary sources of *P. infestans* inoculum originate from infected seed; diseased weed hosts and or plant remain via asexual population (Kamoun and Smart, 2005).

Table1. Some of different strains with different mating type of *P. infestans* in tropical Africa (Tomura *et al*., 2017).

Pathogen type	Strain	Mating type
P. infestans	9173, 9174, PI0-1, PI1234-1	$A1^e$, A1,$A2^e$, $A1^e$ and $A2^e$
Phytophthora sp	32716	$A1^e$
P. vignae	30473, 30613	Homothallic
P. nicotianae	ATCC 38606 and ATCC 38607	(A2 mating type and (A1 mating type)

Host range of the *P. infestans*: There are over 120 host species of the *P. infestans* pathogen including tomato, eggplant, potato and others (Table 2). On those hosts, the pathogen is capable to cause late blight disease at different growth stages and parts of the plants such as tissues, roots, tubers, herbaceous stems, woody trunks, foliages and fruits (Erwin and Ribeiro, 1996). Among these plants, tomatoes and potatoes have been described to be the main hosts of the *P. infestans* while others are described as alternative hosts as shown in Table 2 below. The existence of this wide host range for the *P. infestans* complicates designing of appropriate management options in tomato. There is need to clearly identify the remaining hosts of the pathogens and their associated strains so that appropriate management options may be designed and applied for managing the late blight disease in tropical Africa

Reproduction cycles of the *P. infestans:* The pathogen has two types of reproduction cycles (sexual and asexual), both of which have been described in three stages A-C (Fig 1). In stage A, a fully effective organism is on the host and the pathogen follows either of the two modes of reproduction depending on the environmental conditions (Foolad *et al*., 2008). If it goes through asexual reproduction, the pathogen sporangia germinates and releases zoospores which can then move chemo-tactically (in C) within the environment or directly through sporangia by wind or water. If it follows sexual reproduction in B, the pathogen produces two mating hormones α1 and α2, example for mating type A1 and A2 respectively which aid in the production of oospores (Tomura *et al*., 2017). In stage C, mating of A1 andA2 take place and secreted mating hormones α2 (from A2) and α1(from A1) induce the sexual reproduction of the counter mating types A1 and A2, respectively hence production of oospore.

Infection mechanism of the pathogen and late blight disease development: For the pathogen (*P. infestans*) to effectively infect and colonize its host, a sequence of pathogenic processes is necessary (Fig. 2). In series, the pathogen sporangium or zoospore has to be formed followed by cyst formation, then germination of the cyst/spore to form appressorium which, enhances penetration unto host and infection vesicle, then intercellular hyphal growth and haustorium formation and initiation of sporulation (Huitema *et al*., 2004; Nowicki *et al*., 2013). If these stages are successful, then colonisation on plant can be considered successful otherwise not based on some form of host resistance or interference by some environmental factors such as application of chemicals to control the pathogen or other nature based climatic conditions (Whisson *et al*., 2016).

Table 2. Common hosts *P. infestans* (Erwin and Ribeiro, 1996; Hooker, 1981).

Host	Type of host
Tomato(*L.esculentus*)	Main
Potato(*Solanumtuberos*um)	Main
Tree tomato (*S. betaceum*)	Alternative
Pear melon(*S. muricatum*)	Alternative
7Nolanaspecies	Alternative
Eggplant(*S.melongena*)	Alternative
Wild Solanum species	Alternative
Naranjilla(*S. quitoense*)	Alternative
Datura species	Alternative

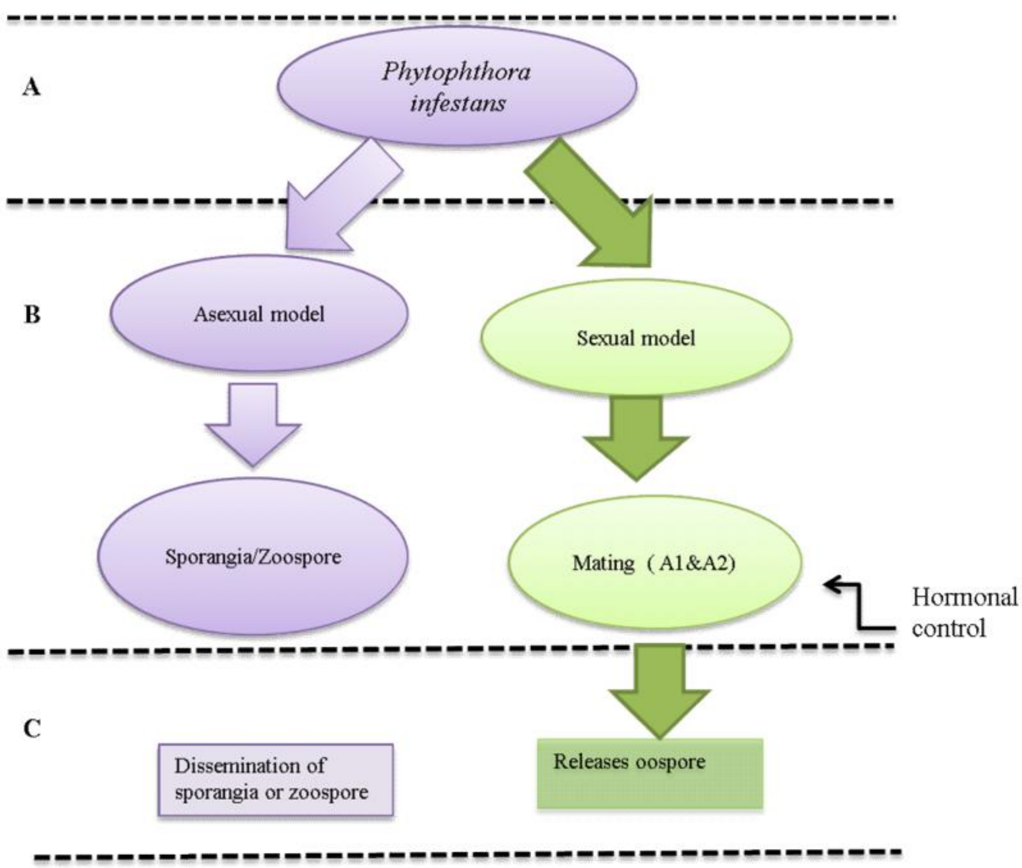

Figure 1. Reproduction of *P. infestans*.

For successful colonisation, the pathogens' infection vesicle is supported by different virulence (AVR) and resistant (R) genes (Huitema *et al*., 2004). In addition, the infection process involves secretion of different protein molecules which enable attachment of *P. infestans* to the host and breaking down physical defence barriers of the host plants (Huitema *et al*., 2004).

On and in the host tissue, *P.infestans* suppresses the plant immunity through secretion of the effector proteins commonly known as apoplastic effectors (those formed on the outside) and cytoplasmic effectors (those formed inside) (Lo Presti *et al.,* 2015). Successful colonisation by the pathogen leads unto symptom development and effects as described in Table 3.

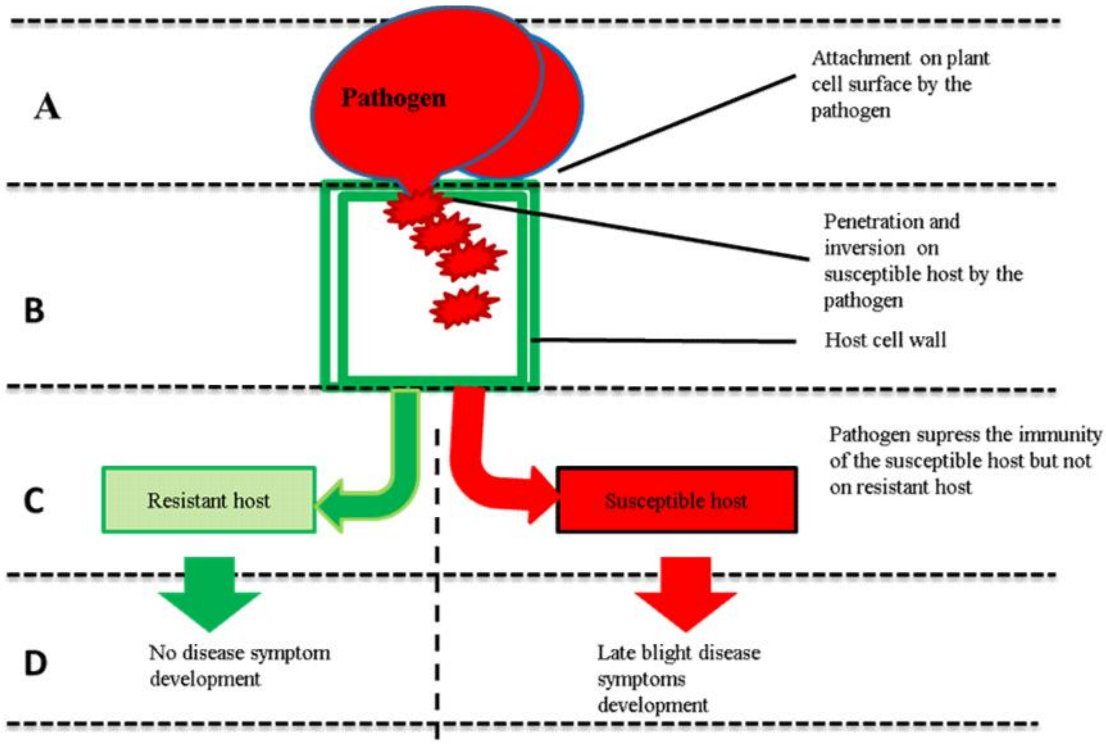

Figure 2. Stages of late blight disease development. In this model, two possibilities can occur upon pathogen contact to host as described in stages A-D. In stage A: The pathogen from different sources attaches the host, B: Invasion stage, C: Molecule exchange between pathogen and host where the pathogen supress the host immunity, D: There is a successful in susceptible variety and fail to colonize a resistant host. In susceptible host cell wall apposition is absent, the pathogen colonizes and supress then develops the late blight symptoms as showed in Table 3 below.

Table 3. Symptoms and or signs incited by *P. infestans* and their effects on different parts of the host tomato plant (Agrios, 2005).

Part of plant	Symptoms and Signs	Effect
Leaves	Necrosis, shrivelling, brown colouration, powdery and whitish rings	Reduced total number of photosynthetic cells
Petiole and stem	Elongated, blackened Water-soaked spots. Lesions covered with a grey	Reduced growth, infected fruitlets
Fruits	Circular greasy lesions A thin layer of white mycelium	Total plant failure to reach maturity

Management of late blight disease: There exist a number of management options that are used against late blight disease (Table 4). The most important ones are as discussed in the sections below.

Cultural control: Cultural practices such as timely weeding, crop rotation, elimination of volunteer tomato plants and planting clean seedling are major components of growers' strategy in disease management; and these methods can sometimes limit the disease development to economical threshold levels. The cultural methods can prove useful in preventing introduction of inoculum to healthy transplants and prevent development or spread of inoculum between and within the field (Agrios, 2005). The principle behind the cultural practises is field sanitation i.e. keeping the field clean (Mpumi *et al.*, 2016). A good example for applicability of this principle include three major practices (1) rogueing, to prevent the spread of diseases from one plant to another (Mpumi *et al.*, 2016) (2) Timely planting, to create unfavourable environment condition for the growth and development of the pathogen and avoiding the rainy season (3) mulching, this is very important method after weeding so as to prevent the spreading of the disease though rain splash. However, in the tropical Africa, there exist challenges is using cultural control options including this approach making it ineffective. The challenges raised include (a) farmers' poor understanding of different factors that could lead to disease build up such use of unimproved susceptible tomato varieties, improper destruction of infected plant debris and continuous mono-cropping, (b) existence of a wide-host range for the pathogen within farms proximity (c) small-scale farming with mixed cropping options and (d) existence of different pathogen strains near or within farmer's field. Therefore, there is need to educate farmers and design specific management recommendation which can be suitable for managing late blight in the complex tropical African environment such as manipulation of planting date, planting density and intercropping that are often used to reduce build-up of air-borne inoculum as well as an escape mechanisms for the late blight disease.

Fungicide application: This is the main approach used at global level in the management of late blight in tomato and potato (Kamoun and Smart, 2005). For the chemical application to be effective, it must be applied before infection (Beckerman, 2008). In the tropical Africa, chemical application is the only most common and preferred approach though not always possible to small scale farmers due to high cost and those who afford it either do not follow recommended rates of application or lack knowledge of handling the chemicals. Common fungicides used in the tropical Africa are chlorothalonil, which is usually applied before or upon disease development and metalaxyl, which inhibit or reduce disease progress once symptoms are apparent due to its ability to inhibit ribosomal RNA (rRNA) polymerases in fungi. The metalaxyl is capable of reducing incorporation of uridine which is the major cause of disease occurrence. Pre-treatment of tomato plants with the chemical such as dl-3-amino-butyric acid induce systemic-acquired resistance in the tomatoes, protecting them from late blight infection through inhibition of haustoria formation and growth of the *P. infestans* hyphae (Binyam, 2014). However, these applications increase production cost and the potential for human health and environmental risks associated with fungicide residual. Some of examples of chemical fungicide reported includes dithiocarbamates, such as mancozeb, which break down into carcinogens causing liver and thyroid tumours, and testicular effects (Novikova *et al*., 2003). Also chemical applications are associated with several challenges mainly, development of resistance by pathogens and also are associated with negative impacts to non-target organisms and pollution to the environment Therefore, alternative method which is economical feasible, health safety and environmental friendly is required in sustainable management of the *P. infestans* pathogen in tomato.

Host-plant resistance: Since the outbreak of the late blight (LB) disease to potato in 1840s, the concern of developing LB resistant potato and tomato cultivars has been of great interest (Nowicki *et al.*, 2012). Since then, research evidence has shown that resistance to *P. infestans* both race-specific resistance (i.e specific, vertical, or "gene-for gene" interaction) and race-non-specific resistance (i.e, horizontal, or partial resistance) can be developed (Nowicki *et al.*, 2012). Some reports show that, tomato with disease resistance ability by vertical resistance have been developed and are effective (at least initially) in avoiding growth and development of pathogen to the crop.

The pathogen has a tendency of re-emergence with more virulent strains leading to more aggressive lineages and this makes the resistance gene to be effective in only one or a limited number of pathogenic races (Fry *et al*., 2013). In comparison to vertical resistance, race-nonspecific resistance is often controlled by several genes or quantitative trait loci (QTLs), which is partial resistance against multiple races of the pathogen. This is always slow and cannot stop the progress of the disease since LB disease spread quickly (Fry *et al*., 2013).

The cornerstone of disease management is the use of resistant crop cultivars but, durable resistance to late blight has not been available to growers, particularly in varieties that are in high demand by consumers (Kamoun and Smart, 2005). As a result, most of different susceptible cultivars are still being grown due to cultural and economic values such as variety popularity, factors which limit adoption of new or resistant varieties such as palatability, colour and shape of fruits). Host resistance to late blight has been reported as an effective strategy in the management of late blight and have long-term economic benefits for small-scale farmers. It also reduces the ability of pathogen to resist fungicide by minimizing changes in the population structure of *P. infestans*

The use of host plants (cultivar) with very high resistance has proved to be helpful in reducing the amount of fungicides (Jones, 1998). Late blight in tomato is controlled by dominant gene (Nowicki *et al*., 2012). For example, Ph-1, a completely dominant gene and is known for conferring resistance against tomato race-0 (T0), however, it was rapidly overcome by new races of the pathogen. The Ph-2 gene provides only partial resistance to tomato plants. A disadvantage is that instead of blocking the disease, Ph-2 only reduces its development rate and hence may not be effective when more aggressive isolates are present. Resistance provided by Ph-3, on the other hand, has been reported to be considerably effective against a wide range of *P. infestans* isolates. In terms of inheritance, both Ph-2 and

Ph-3 display incomplete dominance (Nowicki *et al*., 2012). As reported elsewhere, race change in *P. infestans* in common and has complicated the development of plants which are fully tolerant to this disease. However, tomato varieties reported to have a reasonable resistance to late blight resistance in Africa are not exceptional as they are also subjected to partial protection due to race changes. Therefore, breeding programs should rely on more durable resistance mechanisms such as the introgression of several resistance genes (quantitative resistance)

Therefore, it is vital that during screening for host resistance, it is better to consider farmer preference, high demand varieties, and economical factor so that the developed varieties improve the farmer's challenges faced in LB disease.

Biological control: Researchers have investigated the use of biological control as a potential strategy and solution to the late blight problem. Biological control includes the use of different microorganisms such as bacteria, fungi, nematodes and viruses (Shuping and Eloff, 2017). The great potential use of microorganism in management of late blight disease is based on the antagonistic nature of microbes to *P. infestans* (Shuping and Eloff, 2017). Also, the use of the biological control is environmental friendly, the microorganism are available to the surrounding and its safety in human health. One of the most cited microorganisms that have been used for biological antagonistic against the *P. infestans* include fungi known as *Trichoderma harzianum* (Fatima *et al.,* 2015). The *T. harzianum* has been reported to be effective in reducing incidence of *P. infestans* through secretion of different antifungal substances of various toxic substances and antibiotic metabolites which are involved in the inhibition and lysis of pathogenic fungi (Lorito *et al*., 1993). Other fungi inhibiting *P. infestans* include *Gliocladium spp* and *Penicillium funiculosum* (Fatima *et al*., 2015). Also, there is complementarity of bacteria with biocontrol activity from the genera Bacillus, Pseudomonas, Rahnella and Serratia (Daayf *et al*., 2003). For example, Stephan *et al*. (2005) reported that metabolites from *Bacillus subtilis* have bio control abilities and antagonistic activities against late blight in tomatoes. In view of the reported successes on the use of biological control agents in other parts of the world, similar approach could significantly be deployed in Africa to control late blight disease in Tomato. This is due to the fact that the microbes can easily be isolated from local environments and used sustainably without harm to non-target organisms and environment.

Nevertheless, in tropical Africa, limited information is available on use of biological control in managing late blight disease. The identification of the strain of the *P. infestans* is needed so that to increase the accuracy for the specific microbe or organism to the specific strain of the *P.infestans* rather than general group of pathogen strains with no identification.

Plant extracts: Plant extracts are increasingly being explored for managing plant diseases due to the fact that they are portrayed as environmentally friendly and safe to humans contrast to synthetic fungicide (Goufo *et al*., 2008). They contain active natural chemical that are effective in crop protection against the pathogen (Hubert *et al*., 2013; Ndakidemi and Dakora, 2003; Makoi and Ndakidemi, 2007). Plant extracts are known to produce secondary metabolites such as phenolic/flavonoids and terpenes/monoterpenes which inhibit fungi, bacteria, and insects under laboratory, screen house and field tests (Hubert *et al*., 2013; Ndakidemi and Dakora, 2003).

Studies have shown that the use of synthetic fungicides in managing late blight disease levels were comparable with that of plant extracts in Cameroon and Kenya (Goufo *et al.*, 2010; Lengai *et al.*, 2016). Extracts from different plant such as *Tephrosiavogelli* and *Ageratum houstuianum* among others have been reported to be effective in reducing late blight severity (Goufo *et al*., 2010). Also the extract from *Ocimum gratissimum, Cupressus benthamii* and *Vetiveria zizanioides* have been reported to have inhibitory capacity against the late blight fungal pathogens (Goufo *et al*., 2008; Goufo *et al*., 2010). A study in human model showed that plant extracts from *Sphaeranthus suaveolens*, exhibited remarkable strong antifungal activities. This prompted an idea of their possible action in controlling fungal pathogens such as *P. infestans* in tomato. Although the reported plants were effective against fungal pathogens in plants, screening them against P. *infestans* will reveal their potential in combatting this disease.

The ability and effectiveness of different plant extracts in reducing disease levels in plants has been reported to be related to the mode of action of the plant extracts (Nashwa and Abo-Elyousr, 2013). Some plant extract act directly on the pathogens while others induce systemic resistance in host plants to reduce disease occurrence and development. Also the modes of action of the plant extracts are comparable with those of the synthetic fungicides as previously described and also as per report by (Lengai *et al.*, 2016). As far as tropical Africa is concerned, use of plant extract is based on indigenous knowledge but very little has been documented (Olanya *et al*., 2012). This thus calls for research to quantify use and potential of plant extracts in managing late blight disease in tomato in tropical Africa.

Integrated Disease Management (IDM): Integrated disease management has been cited to be among the best method in late blight disease management in tropical regions where fungal inocula are abundant in most months of the year (*Olanya et al*., 2004). A mode IDM package includes cultural practices (early planting and the use of improved crop variety (early and mid-maturity variety, good crop husbandry), tolerant variety and reduction of frequency of synthetic chemical application (Agrios, 2005). Other examples of the IDM package includes: sowing of disease-free seed; eliminating diseased tomato plants, maintaining weed free environments and minimised chemical sprays. The IDM can also include other different combined approaches consisting of cultural practices; host plant resistance, biological control and others (Makoi and Ndakidemi, 2007) have been reported to help farmers reduce the use of chemical fungicides. Although this approach is always encouraged, proper understanding by small scale farmers on how to create a balance of the procedures especially on which to start and when is always associated with some technical flow that is not always easily adopted in tropical Africa. Thus, there is need to train farmers on how to effectively adopt the IDM techniques, which however calls for research to develop cost effective farmers' based recommendations suitable for managing the late blight in different location in tropical Africa.

Table 04. Management option of late blight disease.

Method(s)	Strengths	Weakness
Cultural	Conserve soil nutrients and recycling through crop rotation and intercropping.	They are effective when used in combination with other
Chemical	Fast effect on pathogens leading to increased yield production.	It is temporary They are not able to cure existing symptoms
Integrated disease management(IDM)	They are cheap options to late blight management.	It depends on a crop production system
Biological	Sustainable and environmental friendly, pathogen specific.	Developing the methodology takes a long time
Resistant varieties	The constitutive defence makes the plant to thicken its cuticle and constitutively produce secondary metabolites which prevent the pathogen from attacking the plant.	Breeding for late blight resistance is a slow process

Conclusion: Worldwide, tomato is considered as the most important vegetable food crop due to its beneficial nutritional and economical roles. However, tomato is highly susceptible to late blight disease causing low production of the crop. In tropical Africa, the disease is a serious challenge to production. Management of the disease is limited by biology, wide host range and environment conditions under which the pathogen works. Despite a number of management options that have been discussed in this review including cultural, resistant varieties, biological, chemical, integrated disease management and use of plant extracts, only one management option (synthetic chemical) is commonly used despite its harmful effect to target and non-target environment and cost involved. However, this review has also shown that use of plants extracts is increasingly important, thus there is need to conduct research on pathogen identification, selected plant in management late blight disease in tomato within the context of tropical Africa.

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