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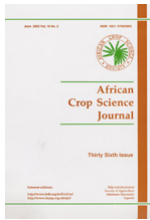
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- FORUM -

Epidemiology and population dynamics of *Phytophthora infestans* in Sub-Saharan Africa: Progress and constraints

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ABSTRACT

Global estimates of losses attributed to plant diseases are approximated at 24.8 million dollars, of this amount 3.4 million dollars has been recorded for potato. Of the potato diseases, late blight (*Phytophthora infestans*) is the most significant constraint in tropical Africa. Variation in losses of potato caused by late blight have been documented in several countries, and has shown that yield losses can range from 30 to 75% on susceptible varieties. In terms of disease cycle, the sources of primary inoculum have not been adequately investigated, however, the continuous cropping of potato and tomato ensures inoculum presence year-around in tropical Africa. Data on the low incidence of tuber blight and the lack of evidence for potato seed-borne infection suggests that tuber blight is not a significant source of primary inoculum in the tropics. Population studies of *P. infestans* in Sub-Saharan Africa (SSA) have been conducted primarily on isolates from Uganda, Kenya and S. Africa. Mating type tests with A1 tester isolates coupled with DNA analysis revealed that the fungal isolates from Uganda, Kenya and S. Africa are of A1 mating type (US 1 clonal lineage). Variation and lack of consistency in oospore production (10 % selfing, 24 % mating, & 15 % non-oospore producers) have been detected among the isolates from Uganda and Kenya. Similarly, variability in metalaxyl sensitivity, has been detected among these isolates. Fungicide and variety reaction studies conducted in Uganda, Kenya and Ethiopia suggests that significant late blight control can be achieved when the protectant fungicide, Dithane (a.i mancozeb) is applied on a scheduled basis. On-farm research also indicates that three timely applications of a protectant or a protectant fungicide alternated with systemic fungicide can be effective for late blight management. Results of in-vitro tuber blight development and host-specificity studies imply that isolates from potato are more virulent than isolates from tomato. Studies are underway to quantify general resistance of potato varieties as well as to monitor the significance of fungal population deviations in the region. Decision support systems are in the process of being developed to optimize fungicide application and variety resistance for late blight management.

Key Words: *Phytophthora infestans*, fungal population, fungicide sensitivity, epidemiology, yield loss, tropical Africa

RÉSUMÉ

Les estimations globales des pertes issues des maladies des cultures sont approximativement de 24,8 millions de dollars dont 3,4 millions de dollars pour la pomme de terre seule. Des maladies de la pomme de terre, le mildiou (*Phytophthora infestans*) est la contrainte la plus significative à la production de la pomme de terre en Afrique tropicale. Les pertes de pomme de terre causées par le mildiou ont été documentées dans plusieurs pays, et il a été démontré que les pertes en rendement peuvent aller de 30 à 75% chez les variétés sensibles. Concernant le cycle d'infection, les causes de l'inoculation initiale n'ont pas été adéquatement élucidées, cependant, la continuité de la culture de pomme de terre et de la tomate est indicative quant à la présence et l'inoculation continue de l'infection en Afrique tropicale. Les données sur la basse incidence de la pourriture rose des tubercules et le manque d'évidence pour l'infection due à la semence de pomme de terre, suggèrent que la pourriture rose des tubercules ne soit pas une source significative de l'inoculation primaire dans les tropiques. Les études des populations du *P. infestans* en Afrique Sub-saharienne (SSA) ont été conduites initialement à partir des isolats de l'Ouganda, Kenya et Afrique du Sud. Les tests de type accouplement avec les isolats du testeur A1 couplés à l'analyse de l'ADN ont révélés que les isolats fongiques de l'Ouganda, Kenya et l'Afrique du Sud sont du type A1 (lignée clonale US1). La variation et le manque de répétabilité dans la production des Oospores (10% uniformes, 24% couplés, 15% sans production d'oospores) ont été détectés parmi les isolats d'Ouganda et du Kenya. De même, la variabilité à la sensibilité au métalaxyle, a été détectée parmi ces isolats. Les études conduites en Ouganda, Kenya et Ethiopie, sur les fongicides et la réaction variétale, suggèrent que le contrôle significatif du mildiou puisse être atteint quand le fongicide protectant, le Dithane, est appliqué à une base régulière. La recherche en milieu paysan a aussi indiqué que trois applications rigoureuses du protectant ou fongicide protectant en alternance avec le fongicide systémique peuvent être efficaces pour le contrôle du mildiou. Le développement in vitro de la pourriture rose des tubercules et les études de spécificité de l'hôte impliquent que les isolats de la pomme de terre soient plus virulents que les isolats de la tomate. Des études sont en cours pour quantifier la résistance générale des variétés de pomme de terre et pour aussi suivre l'importance des déviations de la population fongique dans la région. Des systèmes d'amélioration décisifs sont en train d'être développés pour optimiser l'application du fongicide et la résistance variétale pour le contrôle du mildiou.

Mots Clés: Mildiou, population fongique, sensibilité au fongicide, épidémiologie, perte de rendement, Afrique tropicale

INTRODUCTION

Among all the crops grown worldwide, potato (*Solanum tuberosum* L.), is known to suffer the greatest losses from disease attack (**Table 1**). Late blight of potato, caused by *Phytophthora infestans* (Mont. De Bary), is among its most important diseases, being especially devastating in the major potato growing tropical highlands of Sub-Saharan African. Serious economic consequences often result from complete or partial devastation of infected fields (PRAPACE/CIP, 1996; Sengooba and Hakiza, 1999). The emergence of A1 fungal strains with deviant sexuality and the detection of fungicide resistance in some fungal isolates in potato growing regions of tropical Africa (Erselius et al., 1998) has raised concern for effective disease management. Because of the rapid development of late blight, infections occurring during various stages of crop development represent enormous economic threat. With the exception of optimum or scheduled fungicide applications based on the favourable weather conditions or decision support system, which is still under development in tropical Africa, the most economically viable disease management options is for the use of host-plant resistance.

Occurrence of *P. infestans* has been closely linked to the introduction of potato varieties in many countries of Sub-Saharan Africa (Natrass, 1951; Sengooba and Hakiza, 1999). The introduction of the fungus and its subsequent spread have been accomplished primarily through the movement of potato seed. The major factors affecting potato production such as: use of susceptible varieties, diversity of pathogen virulence and races, lack of adequate disease management tactics and favorable environmental conditions have incidentally and consequently led to perpetuation and increase in late blight disease. Although reports of disease occurrence have been thoroughly documented, to date, paucity of information exists concerning the epidemiology and characteristics of late blight fungal isolates in many countries of SSA. Moreover, the impact of environmental factors on disease development has not been adequately addressed. Studies on the epidemiology and fungal population dynamics are important for designing adequate late blight management tactics. Because of the differences in environmental conditions, and the diversity of the geographical areas in which potato varieties / clones are grown in tropical Africa, it is important to have a sound understanding of the fungal population dynamics and utilise this to design site specific management options. Therefore, the objective of this paper is to review and assess:

- late blight incidence and severity relationships and the impact environmental parameters on late blight development on potato yield loss.
- epidemiology and population dynamics of *P. infestans* in few selected countries of Sub-Saharan Africa.

- late blight management options (host resistance, fungicide, cultural) as well as constraints and prospects for optimum disease management.

MATERIALS AND METHODS

Occurrence of late blight in a few Sub-Saharan Africa countries. Documentation of late blight occurrence on potato has been reported in various countries of Sub-Saharan Africa by a number of researchers. Most of the data have been obtained through survey methodology or in-country reports on potato production. In some cases, data were obtained from observational trials as potato varieties were being introduced. Data have also been compiled through variety or clonal evaluation experiments for late blight resistance. Usually this involves collaborative activities with National Agricultural Research Systems (NARS) with Universities and International Agricultural Research Institutions such as the International Potato Centre.

Late blight have been reported in the potato growing countries of Sub-Saharan Africa ranging from East and Central African countries, to Southern Africa to the West African country of Cameroon (**Table 6**). Disease distribution and severity has been mainly confined to the highland regions (1,800 - 3000 masl) and on potato and tomato hosts (**Table 6**). Variation in disease incidence and severity has frequently been recorded due to climatic variability. Data from various research work on late blight occurrence and incidence or country reports from various national programs are in agreement with this view (PRAPACE/ CIP, 1996).

In late blight survey reports, the spatial distribution of infected plants and fields have documented random pattern of occurrence of the disease. Therefore, this suggests that sources of inoculum and disease dispersal is random instead of originating from a major source. In SSA countries, there is virtually lack of quantitative data on sources of primary inoculum for *P. infestans*. It is often assumed that the year round production of potato or tomato provides a continuous mechanism for inoculum perpetuation or survival in the dry season. However, limited surveys of potato fields conducted during off-season in Kenya and other countries did not reveal any late blight infection (Olanya and Ojiambo, unpubl.).

Late blight incidence and severity relationships and impact of disease on potato yield in Sub-Saharan Africa countries. Similarly, data on late blight incidence and severity relationships to potato yield loss have been quantified from on station variety or clonal evaluation studies as well as on-farm variety trials. The standard methodology have in most cases involved replicated field experiments coupled with the quantification of late blight development, plant characteristics, analysis of late blight disease progression curves and subsequent deduction of associated potato yield. In some cases, the impact of late blight on potato yield have been studied using replicated field experiments conducted either on-farm or on stations. Yield of potato in experimental plots relative to that of the control (fungicide spray plots) are subsequently derived. On farm estimates have been based on various fungicide management scenarios using numerous varieties over the years (PRAPACE/CIP, 1996).

Variation in the incidence and severity of late blight on potato and tomato have been recorded in many locations and countries. In Uganda, studies conducted by Mukalazi et al. (2000) showed that late blight incidence in various countries range from 5 to 85.4 %, while severity was in the range of 27.9 to 81.6% during a two year study (**Table 2**). Variability in disease incidence and severity has been reported in Kenya, Ethiopia and elsewhere in Sub-Saharan Africa countries. The variation of disease incidence and severity may be accounted for by the differences in rainfall patterns between seasons (bi-modal) and years. Variation have also been attributed to susceptibility and resistance of various varieties (Asante, Tigoni, Victoria, Rutuku, Kabale and Awash) grown in many areas, different planting dates (disease escape), and various late blight management practices.

Relationship of environmental factors to late blight development. The impact of environmental parameters on late blight development has mainly been obtained through on station experiments of variety or clonal reactions to late blight. Most of the results have been derivative data since key environmental indicators for late blight epidemics have only been quantified in few central locations in some countries. These parameters often include: temperature, relative humidity, rainfall and hours of solar radiation recorded from the established weather stations located at research stations. In some cases, supplemental weather equipment has been deployed on station for record of additional environmental data.

In tropical Africa, the impact of environmental parameters on late blight development has not been adequately quantified. The geographical diversity of the region and the lack of modern equipment imply that there is need to quantify the driving variables for late blight epidemics. Key climatic variables most often associated with severe epidemic development include relative humidity, rainfall and temperature (Campbell and Madden, 1990; Zadoks and Schein, 1979). Derivative data on cumulative climatic variables from Uganda, Kenya and Ethiopia reveal that late blight development is positively correlated with rainfall amount and relative humidity (Bekele and

Gebremedhin, 2000). However, there is very limited data on the use of micro-climate or environmental monitoring for forecasting the development of late blight epidemics at the regional or local levels.

Impact of late blight on yield loss of potato. Late blight of potato have been one of the most devastating constraints to potato production in tropical highlands of Africa. On station results have documented potato yield loss attributed to late blight in the range of 2.7 to 47 % at Holetta Research Station (Bekele and Hiskias, 1996). At Kalengyere Research Station, yield losses of up to 20 % have been documented in a season with low late blight pressure (Mukalazi et al., 2000). Similarly, yield gain of greater than 20 % have been recorded under on-farm situations in Kiambu, Kenya (**Table 3**). Generally, potato yield loss attributed primarily to late blight is dependent on variety susceptibility or tolerance / resistant and disease management practices.

Population dynamics of *P. infestans* in few selected countries of Sub-Saharan Africa. In Sub-Saharan Africa, characterization of fungal population dynamics have been done mainly on isolates obtained from Uganda and Kenya (Hohl et al., 1998; Mukalazi et al., 2000). In South Africa, extensive research has been conducted using isolates from the Republic of South Africa itself. The determination of fungal mating types in Uganda and Kenya have been conducted by pairing A1 tester isolates with unknown isolates on clarified V-8 agar under laboratory conditions; with subsequent mating type tests done with A2 tester isolates at Cornell University. In these studies, more than 50 isolates collected from diverse geographical locations in Uganda and Kenya were used. Fungicide sensitivity tests have also been carried out using standard procedures (Deahl et al., 1995). In this case, in-vitro studies have been conducted on V-8 medium amended with the fungicide metalaxyl (Ridomil) at various concentrations of (5, 10, 50, and 100 ppm and control) in replicated, well designed experiments. Studies on host-specificity have been conducted on isolates from some countries. In most instances, host-specificity tests were carried on detached leaves of tomato and potato hosts using a combination of fungal strains isolated from either tomato or potato. Similarly, studies on in-vitro tuber blight development have been done with isolates differing in a number of characteristics such as: sensitivity to metalaxyl, oospore production, host of origin and virulence of fungal strains.

Mating type tests revealed that there was no consistency in Oospore production among the isolates from Uganda and Kenya; 15% non-oospore producer, 10 % produced oospores in selfing, and 49 % produced oospores in selfing and mating (**Table 5**). Oospore production in selfing and mating tests suggests that there is potential for genetic variation among these pathogen isolates. It is not known to what extent this variation represents in terms of pathogen virulence and fitness. These results represent same deviation in reproduction biology and genetics of *P. infestans* isolates in which oospore reproduction was thought to occur predominantly through sexual recombination of opposite mating types. Subsequent virulence tests on detached potato leaves conducted with oospore producing isolate, non-oospore producer and a tomato isolate revealed no significant differences except that oospore producing isolates produced larger lesion size diameter (**Table 4**). Further characterisation of fungal isolates from various countries need to be conducted. Similar results were obtained when in-vitro tuber blight development was studied using the same isolates. Similarly, studies on metalaxyl sensitivity showed that three reaction categories (sensitive, resistant and intermediate) were detected among isolates. Approximately 44.4 % isolates resistant and 24 % were sensitive to metalaxyl in in-vitro tests (**Table 5**). This suggests that precautions should therefore be exercised in the application of metalaxyl fungicide for management of late blight in the region. Because the isolates used in population studies are collected from only two countries (Uganda and Kenya), a diversity of isolates from various countries and a wider geographical region is required for complete understanding of population structure in SSA and its implications for late blight management.

Late blight management options. The use of protectant as well as systemic fungicides for management of late blight have perhaps been the most studied aspects of disease management (Lunga'aho, 1998). In tropical Africa, fungicide application intervals, frequency of application and timing, fungicide dose response relationships have been experimented routinely. Fungicide application intervals that have been used include calendar based or scheduled application intervals of 0, 7, 14 and 21 days. Farmer's practices or on-farm fungicide use scenarios often include at least three applications per cropping season. The timing of fungicide application have often frequently been based at the onset of symptom expression.

The use of host plant resistance for management of late blight has received considerable attention in many countries of Sub-Saharan Africa. This has primarily involved the introduction of potato clones from various sources and their evaluation for late blight resistance. This has often involved replicated, randomised experiments conducted under natural late blight epidemics of potato under field conditions.

The use of cultural measures for potato late blight management has been investigated in a number of instances. Management practices include manipulation of planting date for potato varieties in order to avoid period of heavy late blight infection have been investigated. Cultural management tactics also include the use of inter-cropping of non-host crops or low planting density to reduce the spread of fungal inocula.

Prospects and constraints for late blight management in tropical Africa

Host resistance. Integrated management of late blight through the use of resistant potato clones, fungicides, and cultural measures appear to offer the best option for disease management in the tropical highlands of Africa. Management of late blight through host resistance in tropical Africa have been researched by National Potato Research Programmes in collaboration with the International Potato Centre for many years. This involved the utility of potato varieties with variable levels of resistance derived from clones from Population A (high levels of resistance) such as Rutuku, Tigoni, Kabale. Current research efforts are focused on the evaluation of clones from Population B for horizontal or durable resistance. Results of late blight severity levels from national programme evaluation have shown some decreased levels of resistance in some varieties due to increased pathogen virulence, therefore the need for clones with stable and durable resistance.

Fungicide management. Resistant varieties are often used in conjunction with chemical (fungicide) control. Successful management of late blight through the use of foliar fungicides is dependent on several factors such as: proper timing of initial fungicide application, use of effective dosage, timely scheduling of fungicide intervals and adequate coverage of potato foliage. In tropical Africa, contact fungicides such as Dithane M-45 (mancozeb) and systemic fungicide Ridomil (metalaxyl) are used in many locations. Limited use of newer compounds such as Tatoo C (propamocarb hydrochloride), Acrobat (Dimethomorph) and Curzate (cymoxanil) for their anti-sporulant and curative activity on *P. infestans* have been investigated in some countries. In general, there are still very limited advances in fungicide application methodology and technology in tropical Africa. There is limited information on the use of environmental monitoring to aid in proper or adequate fungicide use and application technology. Data on decision support system to optimize fungicide use in conjunction with resistant varieties is still lacking.

Cultural measures. Cultural measures for late blight management in tropical Africa have been used in various ways. Because potato culls or residue and volunteer plants, and infected tomato plants are sources of inoculum, their elimination will greatly reduce late blight risk. Manipulation of planting date, planting density and inter-cropping are often used as escape mechanism or to reduce build up of air-borne inoculum. Hilling of potato plants, dehauling or vine kill to minimise tuber borne infections are most often used in tropical Africa. The removal of volunteer potatoes, infected tomato plants or spot treatment of pockets of disease development is hardly used by farmers at all. There is, however, paucity of quantitative data concerning the contribution of these sources of inoculum to disease epidemiology in tropical Africa. There are virtually very limited use of containment policy or regulatory procedures that deal with late blight. In general, specific tolerance level for late blight and visual inspections have proven inadequate for disease management in potato.

We conclude that studies on the epidemiology and population dynamics of *P. infestans* in tropical Africa have been constrained by several factors. The bio-diversity and national sovereignty rights as well as the phytosanitary regulations that limit the movement of pathogen isolates, will enable the phenotypic, pathological and comparative studies of diverse isolates from many SSA countries to be a difficult task. Inadequate laboratory and growth chamber facilities especially in molecular characterization are often a limiting factor in pathogen population studies. The geographical diversity of tropical Africa and the momentous task for any environmental monitoring has been a limiting factor in the development and use of decision support systems for the optimisation of fungicide spray or utilisation in late blight management. However, advances in fungicide application, cultural management in addition to the use of resistant varieties has facilitated late blight management by the small-scale potato farmers. As improvements in host-plant resistance continues and the quantification and utility of general resistance (stability and durability) receives considerable attention, we are optimistic that optimum late blight management and increased potato production will continue in tropical Africa.

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TABLE 1. Global estimates of losses attributed to plant diseases in selected crops worldwide

Crops	Losses in production (%)	Actual losses in production (millions	Value of loss (\$ billions)
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		of tons)	
Potato	21.8	88.9	3.4
Wheat	9.1	33.3	2.2
Rice	8.9	39.4	3.2
Maize	9.4	32.7	1.6
Other cereals	8.6	29.9	1.7
Vegetables	10.1	31.1	2.3
Oil crops	10.2	13.5	1.6
Fiber/rubber crops	11.8	3.1	1.5
Sugar beet/cane	16.5	232.3	2.3
Stimulants	14.9	2.6	1.7
Fruits/citrus /grapes	16.4	32.6	3.3

Source: James (1981)

TABLE 2. Incidence and severity of late blight of potato in Kenya and Uganda during 1998 and 1999 cropping seasons

Districts/location	1998		1999	
	Incidence (%)	Severity (%)	Incidence (%)	Severity (%)
Kenya				
Njambini	67	56	35	15
Mau Narok	91	78	70	40
Mt. Kenya	54	40	30	20
Meru	84	62	50	35
Kiambu	35	20	-	-
Uganda				
Kisoro	85.4	20.4	52.1	7.1
Kabale	95.2	39	81.6	31.8
Mbarara	23.6	9.7	27.9	6.4

Mbale	5	4.5	66.9	19.7
Mean	60.0	37.1	51.6	21.9

Source: Hohl (1998), Mukalazi *et al.* (2000)

TABLE 3. Yield of potato varieties under late blight pressure in Kiambu district, Kenya (on-farm trials) in 1998

Variety	# Fungicide sprays ^x	Yield (t ha ⁻¹)	Yield loss (%)
Tigoni	1 spray	37.98	10.8
	2 sprays	46.45	18.55
	3 sprays	43.88	15.98
	Control (no spray)	27.9	-
Kenya Dhamana	1 spray	29.70	8.17
	2 sprays	33.80	12.27
	3 sprays	33.80	12.27
	Control (no spray)	21.53	-

Source: Njuguna *et al.* (1998)

^xProtectant fungicide Dithane -M45 was used in all experiments

TABLE 4. Susceptibility of potato varieties to late blight infection of detached leaves by three *P. infestans* isolates at 18 C, in growth chamber

Variety	Mean lesion diameter (cm) caused by <i>P. infestans</i> isolates		
	1006x	1017y	LT999z
Tigoni	1.20	1.90	1.60
Asante	1.37	1.95	1.60
Genet	1.31	2.10	1.50
Kerr's Pink	1.30	2.21	1.53
Murca	1.29	1.43	1.64
Mean	1.20	1.90	1.60

^xNon-oospore producer, ^yoospore producer and ^ztomato isolate

TABLE 5. Mating type, oospore production and metalaxyl sensitivity of *Phytophthora infestans* isolates obtained from various geographical regions of Uganda and Kenya during 1997 to 1999

	Oospore production

Location	Isolate designation	Mating type	Oospore production in mating	Oospore production in selfing
Kenya	1001	A1	10	0
Kenya	1004	A1	4	0
Kenya	1011	A1	0	2
Kenya	1026	A1	0	> 1000
Uganda	2014	A1	9	0
Uganda	2027	A1	3	0
Uganda	2002	A1	0	12
Uganda	2034	A1	0	> 150
	Kenya		Uganda	
Metalaxyl sensitivity	Number	% of isolates	Number	% isolates
Resistant	30	86	17	59
Intermediate	3	8	7	24
Susceptible	2	6	5	17
Total	35	100	29	100

TABLE 6. Late blight occurrence and population structure (mating type and hosts) in some countries of Sub-Saharan Africa

Countries	Mating type	Hosts	References
Kenya	A1	<i>S. tuberosum</i> , <i>incanum</i> <i>Panduraforme</i> , <i>indicerm</i>	CIP Ann. Report, 1997-98
Uganda	A1	<i>S. tuberosum</i> , tomato	Kori, 1972, CIP Ann. Report, 1997-98
S. Africa	A1	<i>S. tuberosum</i> , tomato	McLeod and Denmer, 1997
Ethiopia	?	<i>S. tuberosum</i> , tomato	Borgel, 1980; Kidane-Mariam, 1980, unpubl.
Tanzania	?	<i>S. tuberosum</i> , tomato	Natrass and Ryan, 1951
Cameroon	?	<i>S. tuberosum</i> , tomato	CIP Ann. Report, 1972, Foncho, 1982
Rwanda	?	<i>S. tuberosum</i> , tomato	Natrass and Ryan, 1951; Turkensteen, 1988

Burundi	?	<i>S. tuberosum</i> , tomato	Natrass and Ryan, 1951; Turkensteen, 1988
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