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REVIEW

Potato Breeding for Late Blight Resistance in Central and East Africa

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ABSTRACT

Potato late blight is a disease of great loss, which can go beyond 75% in Central and Eastern Africa. With this in mind, in order to limit the excessive use of synthetic fungicides, the use of resistant varieties is a better alternative. This study focuses on the synthesis of works already carried out in the improvement of potato resistance to late blight in Central and East Africa in order to have a general overview. For this purpose, 76 documents were consulted, including 67 scientific articles, eight books, and a web page. The literature has shown that the improvement of potato resistance to late blight in these areas is mainly based on conventional methods throughout the breeding scheme. These studies are mainly led by the International Potato Center. This review covers yield losses due to late blight, the biology of *Phytophthora infestans*, late blight management methods, the genetics of late blight resistance, genetic resources for late blight resistance in Central and East Africa, screening methods and breeding approaches for potato late blight resistance.

Keywords: Central Africa, East Africa, *Phytophthora infestans*, Potato breeding.

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1. Introduction

The potato is the main non-cereal food commodity; it is the fourth in importance and production globally after rice, wheat, and corn. In Central and East Africa, its production in 2021 was estimated respectively at 1,003,942.62 tones over an area of 117,132 ha and 7,944,135.67 tones over 763,066 ha [1]. It is a staple crop with great economic importance in these regions of Africa [2], [3].

Despite all its advantages in these regions, it faces certain constraints, of which diseases constitute the major ones, Bacteriosis, and late blight being the most important diseases [3]–[5]. For late blight, it is a disease of great losses which can go beyond 75% in these two regions [6], [7]. Efforts have already been made to combat this disease. Chemical control is the most used method [8], [9]. Synthetic fungicides have several advantages, including effectiveness, easy application, and a broad spectrum of control. However, some of them are toxic to humans and damage the environment [10].

One of the alternatives to the excessive use of these fungicides against late blight is the use of resistant varieties. This control method makes it possible to reduce the quantity of fungicides and is economical for small producers [11]. Several efforts have already been made in the development of resistant varieties in Central and East Africa with major contributions from the International Potato Center [12], [13]. It is with this in mind that this research sets out to take stock in the form of a summary review on efforts in improvement potato against late blight in Central and East Africa.

2. Yield Losses Due to Potato Late Blight

Late blight is one of the most important potato diseases and has already been the subject of several studies worldwide [14]. In historical terms, it was the basis of the famine in Ireland. A third of the harvest in 1845 and almost all in 1846 and then in 1848 were devastated by late blight [15]. It attacks all parts of the plant, from foliage to tubers [16]. Varying values of losses due to potato late blight have already been reported in several countries, ranging from 30% to 75% on susceptible varieties [17]. Especially in Central and East Africa, in Cameroon, yield losses were 27% to 52% in Dschang and 25% to 71% in Bansoa [6]. In Rwanda and Burundi, yield losses due to potato late blight can be estimated at 75% in the event of no fungicide

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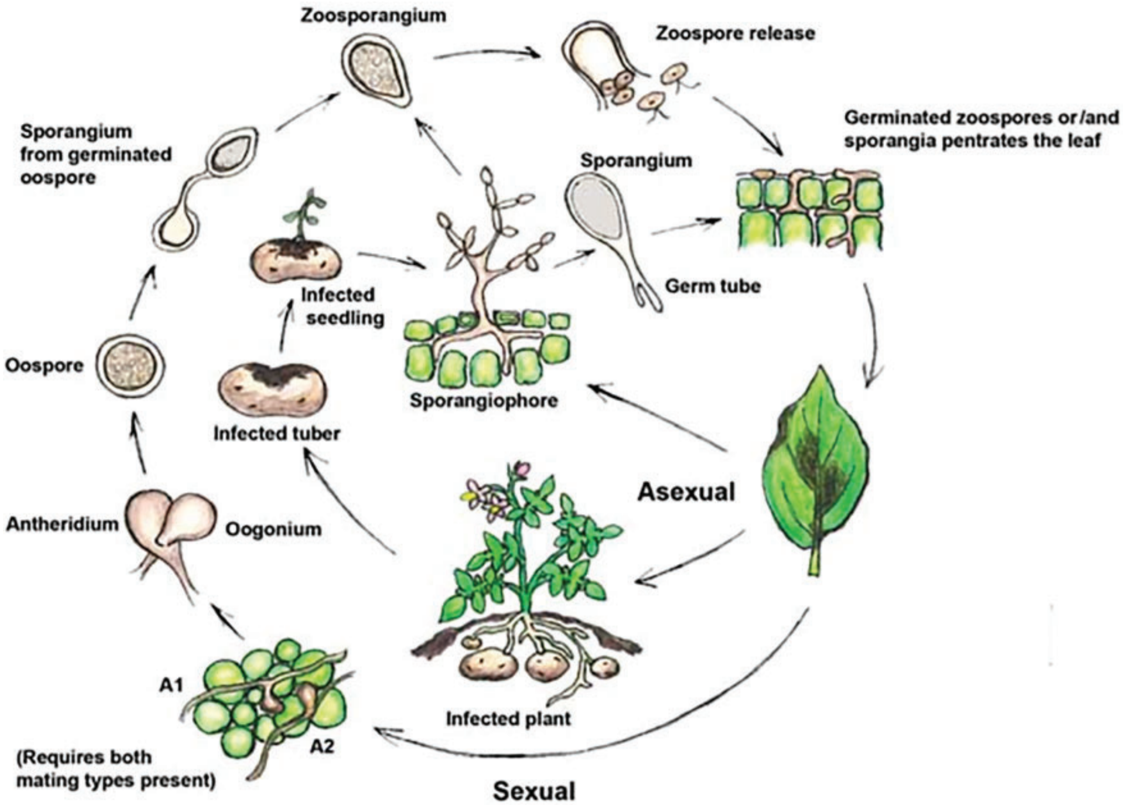

Fig. 1. Life cycle of *P. infestans* [20].

treatment [7]. In Uganda, yield losses from this disease are between 40% and 60% [8].

3. Biology of Phytophthora infestans

3.1. Life Cycle of *P. infestans*

The *Phytophthora infestans* is a coenocytic oomycete with diploid nuclei. This shows that it is not a true fungus. Oomycetes lack chitin in their cell walls and produce short-lived, motile, biflagellate zoospores [18], [19].

Phytophthora *infestans* has two modes of reproduction. In the asexual mode, *P. infestans* produces ellipsoid-shaped spores called sporangia. These are produced at the branch tips of sporangiophores growing in an alternative manner from infected tissues [20]. They disperse throughout the area and can thus reach plants located at a distant distance. Sporangia can also be transported by water to the foliage or tubers of neighboring plants [21], [22]. Infections of the aerial or underground parts are initiated by the sporangia either directly with a germ tube or indirectly by the release of zoospores [23]. After penetration, *P. infestans* forms specialized hyphae that extend from the location of penetration and begin intercellular colonization of tissues. For the sexual mode, two compatible types A_1 and A_2 of *P. infestans* ensure reproduction. The spores produced by sexual mating are called oospores [24]. Both types of compatibilities must infect the same plant or tuber for oospores to be produced. Oospores have thickened walls and survive in soils for several years in the absence of living hosts [14], [24]. Fig. 1, describes the life cycle of *P.infestans*.

3.2. *Symptoms of Potato Late Blight*

The first manifestation of late blight is observed on the leaves of the lower layer, with small pale green to dark green spots that change to brown or black lesions depending on freshness and high relative humidity. A pale green or yellow margin, a few millimeters wide, separates dead tissue from healthy tissue. In high humidity and low temperatures, lesions develop rapidly, and sporulation is visible on the underside of leaves, which is white mycelium. On the stem and petioles, it is a secondary infection from the leaves. The lesions are visible and weaken these parts. On the tubers, superficial and irregular discoloration is observed. Dry, brown necrotic lesions appear on the surface in tubers [16].

4. Potato Late Blight Management Methods

Prophylactic control aims to reduce the primary sources of infection, which are the pile of waste and the regrowth of potatoes in the field. Good cultural practices such as early planting help manage late blight. Likewise, moderate use of nitrogen and the use of reasonable fertilization are often recommended to delay the development of late blight [25]. The use of resistant varieties is considered the best alternative because it is economical in terms of reducing the use of synthetic fungicides [26]. Chemical control has become the most widely used by spraying synthetic fungicides [8], [9], [27]. In biological control botanical, animal extracts and certain microorganisms are used to manage this disease [28], [29]. Fungicides used by countries in Central and East Africa are described in the Table I.

TABLE I: Fungicides used Against Late Blight in Central and East Africa

Countries	Fungicides used	References
Cameroon	Ridomil Plus, Mancozeb 80 WP, Penncozeb 80 WP, Jumber D, Orvego	[30], [31]
Rwanda and Burundi	Ridomil Gold, Emexyl, Victory 72 WP, Safari max, Safarizeb, Mancozeb 80 WP, Benlate, Syngenta Crop Protection, Dithane M 45	[32], [33]
Kenya	Milraz, Ridomil Gold, Acrobat, Penncozeb 80 WP, Antracol 70 WP, Dithane M 45	[34]
Uganda	Dithane M 45, Ridomil Gold, Agrozeb 80 WP, Agro-Laxyl MZ 63.5 WP, Tata master 56 Indofil M45, Greenzeb 80 WP	[8]

5. Genetic Mechanisms of Potato Late Blight Resistance and Gene Action

5.1. Genetic Mechanisms of Potato Late Blight Resistance

For potato, resistance to diseases and parasites is ensured by R genes. The R genes for resistance against *Phytophthora infestans* in potato encode proteins of the NB-LRR class where NB means Nucleotide Binding and LRR: leucine-rich-repeat. It consists of a nucleotide-binding (NB) domain and a leucine-rich repeat (LRR) domain [35]. The LRR domain recognizes pathogenic effectors, and the NB domain initiates the hypersensitivity response [36].

5.2. Gene Action on Resistance to Late Blight in Potato

To understand gene action on a trait, general combining ability (GCA) and specific combining ability (SCA) are powerful tools used. General combining ability defines the average performance of a genotype in a series of hybrid combinations. Specific combining ability (SCA) is the deviation from the expected average of the progeny based on GCA. GCA is due to the additive effects of genes as well as the additive × additive interaction. The SCA is due to non-additive effects and epistatic interactions [37]. Additive effects must be preponderant over non-additive effects for quantitative resistance in order to make it sustainable [38], [39]. In Uganda and Ethiopia, studies have shown a predominance of additive effects over non-additive ones, showing that genetic gains can be made by selecting superior clones [40], [12]. This predominance of additive effects has already been proven by other studies [41]. Results of non-additive effects (SCA) equal to additive effects (GCA) in the expression of resistance to late blight in potatoes were shown by [42]. Furthermore, non-additive effects predominate over additive effects have been found by other researchers [43].

5.3. Gene Diversity for Improvement of Resistance Against Potato Late Blight

Late blight being is one of the most widespread and most studied potato diseases [14], the literature also indicates a diversity of resistance genes to late blight in potatoes [44]. In ancient times, selection against potato late blight was based on the introgression of dominant genes for this trait (from R1 to R11). Currently, to make resistance against potato late blight sustainable through horizontal resistance, minor genes are used. They are combined in a single genotype to avoid rapid circumvention by *Phytophthora infestans* [45]. The most widely exploited currently are the Rpi and RB genes [46], [44]. Their main source is wild species. More than 70 Rpi genes have already been mapped [44].

6. Potential Genetic Resources to Potato Late Blight Resistance in Central and East Africa

Central and East Africa benefit from the work of the International Potato Center (CIP), which works in these areas. Since 1990, the CIP has been working on horizontal resistance against potato late blight [39]. With this aim of improving the quantitative resistance of potato to late blight, the CIP developed two populations, the first of which contained R genes (population A) and the second lacking R genes (population B). The following species were used as a source of horizontal resistance genes: *S. tuberosum, S. demissum, S. andigena, S. phureja, S. acaule and S. bulbocastanum*. However, to avoid the masking of minor genes by the major ones R, in population A, genotypes not containing the latter were selected to form population B. Recurrent selection by crossing the best genotypes of these two populations after three cycles has allowed to obtain the B3 population with the higher and stable horizontal resistance. The clones selected from this population with stable resistance constitute the main source of resistance to late blight in Central and East Africa [41], [42].

Some CIP genotypes that have been used in the potato late blight improvement program in Central and East Africa and some gene source varieties are presented in Table II.

7. Screening Methods for Potato Late Blight Resistance

To target resistance to late blight in potato, we proceed by testing detached leaves in the laboratory, screening in greenhouses, in open fields, and by molecular markers [49]–[52]. The detached leaf test consists of placing the disinfected leaves in the Petri dish and placing the inoculum on their underside. The evolution of the lesions makes it possible to assess the resistance of the genotypes considered [50]. For greenhouse screening, the genotypes to be tested are planted in a greenhouse and then inoculated. The number of days of inoculum application after planting varies from one researcher to another, but several studies have shown that inoculation is done before flowering, around 40 days after planting, and the evaluation of the attack is carried out on the basis of a rating scale in order to calculate the progression curve of the disease [52], [53]. In the open field, the genotypes to be screened are exposed to the pathogen without any fungicide treatment. The process

TABLE II: Potential Sources of Potato Late Blight Resistance Genes in Central and East Africa

Genotypes	Sources	User countries	rAUDP (%)	References
396026.103	CIP	Uganda	–	[12], [47]
396038.107	CIP	Uganda, Ethiopia	36.5	[12], [47]
395011.2	CIP	Uganda, Ethiopia	22.9; 25	[12], [47]
393220.54	CIP	Uganda	15.9	[12]
392657.8	CIP	Uganda	14.1	[12]
393371.58	CIP	Rwanda	–	[13]
393280.82	CIP	Uganda, Rwanda	–	[12], [13]
395015.6	CIP	Ethiopia	29	[40]
395109.34	CIP	Ethiopia, Uganda	21	[12], [40]
396004.263	CIP	Ethiopia	18	[40]
395017.229	CIP	Ethiopia	23	[40]
396264.14	CIP	Ethiopia	18	[40]
395017.14	CIP	Ethiopia	21	[40]
Sarpo mira	Introduction	DRC, Kenya, Uganda	–	[48]

by artificial as well as natural inoculation can be done, and the rating of the disease is done on the basis of the scale [54]. Another screening method is molecular marker-assisted screening. Several markers linked to resistance genes against potato late blight have already been developed [55], [56]. It is essentially based on the polymerase chain reaction (PCR). After extraction of total DNA and electrophoresis, the presence of the marker is sought by analyzing the DNA bands. The absence and presence of the marker are scored binary, 0 and 1 or – and + [49], [57]. Table III presents the screening methods used in Central and East Africa.

8. Improvement Approaches for Potato Late Blight Resistance in Central and East Africa

Several efforts have already been made in the improvement for qualitative and quantitative resistance [62]–[64]. Strength improvement can follow two methods, the conventional method and the modern one.

8.1. *Conventional Improvement*

8.1.1. *Parents' Choice*

The program begins with the choice of parents by screening in the field, in the laboratory or by molecular markers [50], [58]. The choice concerns the genetic diversity of the germplasm and the desired traits (resistance to late blight and high yield). It constitutes the crucial aspect to prevent homozygosity and guaranteed the high allelic diversity of the offspring. Parents are often selected based on their phenotype rather than their genotype, and crosses are made based on trait complementarity. Parents can also be chosen by the test cross model. Thus, parents with the right combining ability are chosen in the improvement program [65].

TABLE III: Screening Methods for Late Blight Resistance in Central and East Africa

Screening methods	Country	References
Field screening	Uganda, Rwanda, Kenya, Cameroon,	[34], [58], [59], [60]
Greenhouse screening	Uganda	[61]
Detached leaves	–	
Screening assisted by molecular markers	–	

8.1.2. *Crossing Models Used*

Crosses are carried out between resistant and susceptible parents two by two by emasculating the flowers of female plants and depositing the pollen grains on the stigma two days later [37]. Several crossing models have already been used in the potato late blight resistance breeding program, including the biparental model [63], [66] the North Calorina design II [12], [67], Line tester, diallel [13], [38], etc.

8.1.3. *F1 Development and Selection*

The potato being autopolyploid, the tubers of the plants resulting from the seeds after crossing constitute the F1 with the segregation of the character [65]. These tubers are vegetatively cloned for multiplication [65], [68]. Selection is done by exposing the F1 and the parents to *P. infestans*. The strongest and most productive are kept to move on to preliminary trials and then into advanced trials [12], [68]. Recurrent selection is carried out to improve populations [41]. The general scheme of conventional potato breeding is illustrated in Fig. 2.

8.2. *Marker-Assisted Selection for Potato Late Blight Breeding Resistance*

The use of molecular markers is of great importance in plant breeding. It facilitates the introgression of a gene of interest and reduces selection time [37]. The use of molecular markers for genes of interest in breeding can accelerate the process of creating cultivars with improved traits. Marker-assisted selection (MAS) has already been established in potato and focused on resistance to pathogens and pests. To make potato late blight resistance durable, it is necessary to combine several resistance (R) genes and/or quantitative trait loci (QTL) against *P. infestans*. This requires the use of molecular markers [55], [56]. Efforts have already been made in the use of molecular markers for the improvement of resistance against potato late blight [63], [70]. Molecular marker technologies and construction of gene maps by linkage have made it possible to detect loci associated with complex traits. Several

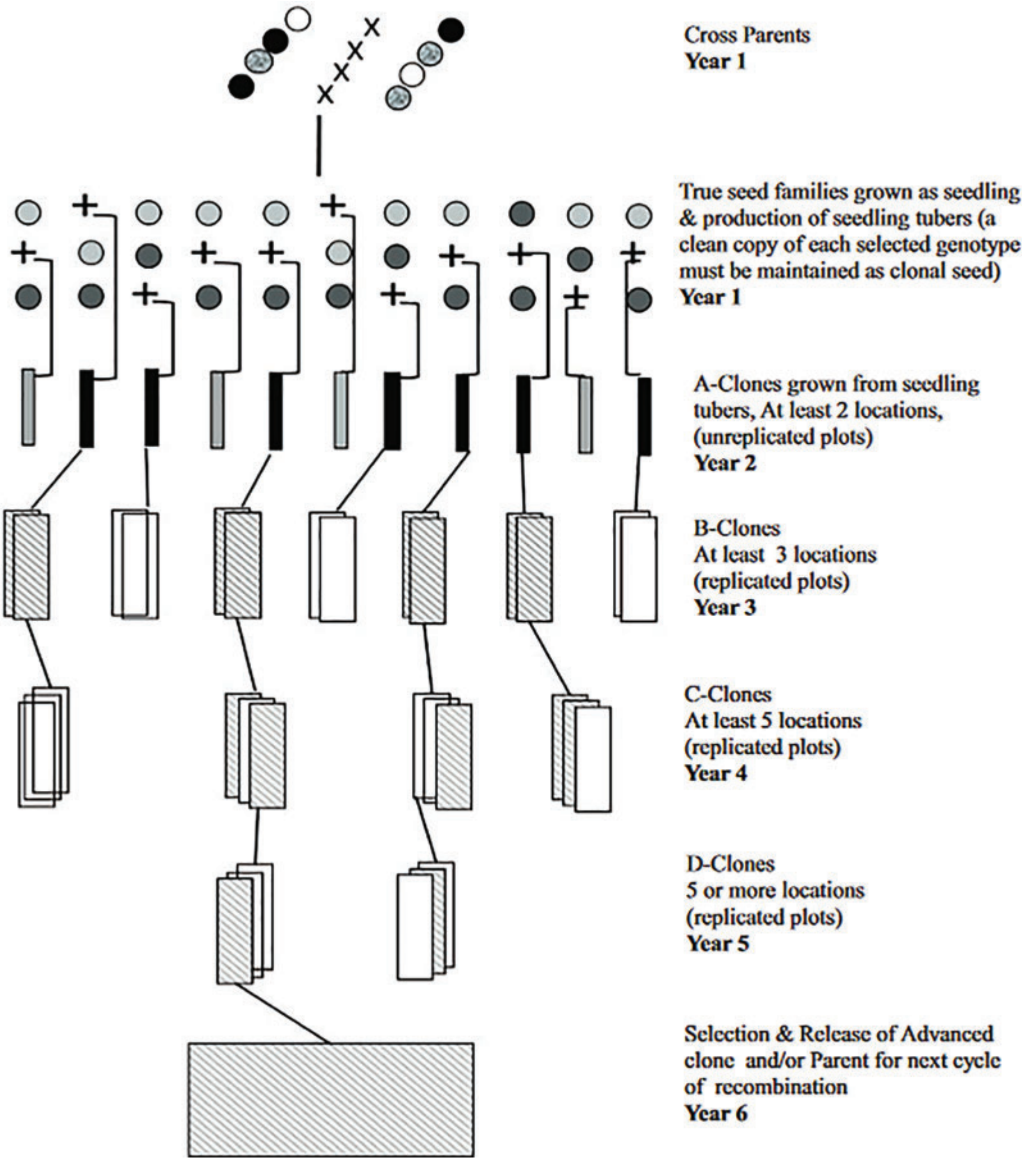

Fig. 2. General outline of conventional potato breeding [69].

QTLs for resistance to potato late blight have already been identified in different species [44], [71]. Likewise, cloning and isolation of particular genes have already been carried out [63], [66]. The other form of use of molecular markers is literature-based marker assisted selection (Background Marker assisted selection) [72]. Several studies have used this MAS pathway to select in the population resulting from a biparental cross, gene pyramiding, the backcross of individuals having acquired the genes of interest. It is essential based on PCR using molecular markers already developed and validated [73]–[75].

In Central and East Africa, it is mainly the conventional method that is used to improve resistance against late blight [12], [13], [42]. CIP work recently genetically transformed the Victoria variety by transgenesis with three resistance genes (RB, Rpi-blb2 from S. *bulbocastanum*, and Rpi-vnt1.1 from *S. venturii*) for resistance to late blight potato [76].

9. Conclusion

The use of resistant varieties is one of the great alternatives to the use of synthetic fungicide. This review aims to summarize the efforts already made in the context of improving potato against potato late blight in Central and East Africa. In view of this review, in these regions, it is the conventional method that has until now been used to improve resistance to late blight. It is used in the population screening phases to choose parents and in selection after hybridization to identify resistant descendants. The use of molecular biology techniques and biotechnologies is low in Central and East Africa in the improvement scheme against potato late blight. The sources of resistance are essentially the populations resulting from the selection of the International Potato Center.

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Conflict of Interest

The authors declare that they do not have any conflict of interest.

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