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Potato virus Y (PVY) and potato virus X (PVX) resistance breeding in Kenya: applicability of conventional approaches

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ABSTRACT

Potato virus Y (PVX) and *potato virus X* (PVX) are among the most important viruses of the potato (*Solanum tuberosum L*.) crop worldwide. The use of virus resistant varieties is considered the most effective and sustainable long term way of minimizing crop losses associated with the viruses. In Kenya, major potato varieties grown do not have effective host resistance to the two viruses. Among the different types of virus resistances available, extreme resistance has been found to be durable and most effective. This type of resistance protects the plant against all strains of the virus and has been found particularly for PVY and PVX. Nature of inheritance of extreme resistance genes make it easy to transfer to cultivated varieties through conventional cross breeding. Screening for the two viruses is cheap, simple and straight forward due to the fewer number of genes involved. In major potato breeding programmes around the world, this type of resistance has been incorporated in many cultivated potato varieties with reported reduction in yield losses. Focus on sourcing of suitable parents, hybridization and screening for the two viruses can make a significant contribution in management of the two locally important viruses while reducing virus related crop losses.

Key words: *Potato virus Y* (PVX), potato *virus X* (PVX), extreme resistance, breeding, Kenya

INTRODUCTION

Management strategies of potato viruses in Kenya

Different authors have reported high levels of susceptibility to viruses in major potato varieties grown in Kenya with corresponding major yield losses (Machangi *et al.,* 2004; Nyaga, 2008; Muthomi *et al.,* 2009; Onditi *et al.,* 2011; Schulte-Geldermann*et al.,* 2012). Majority of farmers in Kenya are smallholders whose knowledge of virus management is often limited (Gildermacher *et al.,* 2011).In addition, certified seed tubers have been costly and scarce (Gildermacher *et al.* 2011) due to high incidence of diseases, mainly viruses in seed production systems (Nderitu and Mueke, 1986; Machangi *et al.,* 2004; Muthomi *et al.,* 2009).

Six major potato viruses are known to be affecting seed quality in the Kenyan seed system: *potato virus* Y, *potato virus* X, *potato leaf roll virus* (PLRV), *potato virus M* (PVM), *potato virus A* (PVA) and *potato virus S* (PVS) though PVY, PVX and PLRV are considered more important due to major role they play in crop losses (Lung'aho *et al.,* 2007; Olubayo *et al.,* 2010). It is estimated that only approximately 1-2 % of seed tubers planted are certified (Kanguongo *et al.,* 2008). As a result of such virus infections, the average crop production has been as low as 7 T/ha (Kaguongo *et al.,* 2008) compared to the Kenyan research conditions where potato production have been found to be 30-50T/ha (Lung'aho *et al.,*2006; Onditi *et al.,*2012). This has prompted a search for sustainable strategies for managing viruses and virus vectors.

The most traditional method of controlling potato viruses has been to spray against aphids which are the major virus vectors (Salazar, 1996; Lung'aho *et al.,* 2007). This strategy has been faulted for being far too expensive mainly for small holder farmers apart from being harmful to the biological ecosystem (Nyaga, 2008). Positive seed selection (selecting less virus infected healthy looking plants as seed for the subsequent seasons) has been successfully promoted with significant yield improvement (34%) using popular local varieties (Gildemacher, 2011). This strategy appeared relevant since it is cheap considering the high cost of seed (50 % of the cost of production) and scarcity of certified seed tubers (Gildemacher, 2012). Elimination of infected seed lots at early stages of seed production minimize sources of virus innoculum in seed potato fields after testing using sensitive techniques such as enzyme linked immuno-sorbent assay (ELISA) (Hinostroza, 1981; Salazar, 1996). Observing sanitary procedures in seed production systems, such as avoiding unnecessary contact, injury and bruising of plants can reduce virus transmission of viruses like PVX and PVY and PVS which are transmitted by exposure to the sap of infected plant (Kabira *et al.,* 2006; Lung'aho *et al.,* 2007). Other recent strategies have been the use of border crops, synthetic insecticides, mineral oil and plant extracts which have also been effective in minimizing virus vector populations (Olubayo *et al.,* 2010). With high incidence of potato viruses in farmer's fields, major decision makers in the potato industry advice farmers to replace their infected seed with certified seed tubers to improve the quality of their seed (MoA/GTZPSDA, 2009) though this has not been practical with high cost and limited availability of certified seed tubers.

Why PVY and PVX resistant potato varieties in Kenya?: Since introduction of the crop into the country over a century ago, very little attention given to development, screening and release of varieties with effective and durable form of resistance to PVY and PVX in addition to other locally important traits (Onditi, 2008; Onditi *et al.,* 2011)). In the latest variety releases in the year 1998, 2002 and 2010, major focus has been to improve tuber yield, cooking and processing quality and late blight (*Phytophthora infestant*) resistance (Lung'aho*etal.,*2006; Onditi *et al.,*2012) than virus resistance despite its importance in seed potato systems (Onditi, 2008; Gildermacher *et al.,*2011). Fortunately, effective types of resistance (immunity or extreme resistance) to potato viruses have been found for PVY and PVX, which protects the plant against all strains of the virus (Wiesema, 1972; Bradshaw and Mackay, 1994). This type of resistance has been incorporated in potato cultivars to reduce yield losses (Hide and Lapwood, 1992).

When field evaluations are conducted on genotypes with this type of resistance, only a small percentage (2-8%) of plants tested using ELISA are found infected with the virus compared to susceptible cultivars where up to 100% of the plants are likely to be infected after three cropping seasons (Davies *et al.,* 1975; Solomon, 1978; Hinostroza, 1981). Using varieties with such resistance in addition to resistance to other impotent viruses would enable seed producers and farmers grow their crop for more generations without lowering seed quality and ware potato yields (Rahman *et al.,* 2010).

The viruses: PVY and PVX: Potato virus Y is a virus species in the genus *Potyvirus*. The main strains of PVY are PVY^{O}, PVY^{N} and PVY^{C} (Upeksha *et al.,* 2012). PVY^{O} is the common strain causing mosaic symptoms while PVY^{C} causes stipple streak and PVY^{N} is a necrotic strain which generally causes mild foliage symptom (Whitworth *et al.,* 2012). Mixed infections of different strains usually produce hybrid strains i.e. $PVY^{N:O}$ and PVY^{NTN} (Beczner *et al.,* 1984; Singh *et al.,* 2008; Barker *et al.,* 2009; Whitworth *et al.,*2012). The most important vector of PVY potato viruses are aphids especially *Myzus persicae* which transmits the virus in a non-persistent manner (Ragsdale *et al.,* 2001). PVY can also be transmitted mechanically by machinery, tools or while walking through the field or from the mother plant through infected tubers (Salazar, 1996).

PVX is a virus species in the genus *Potexvirus*. The main strain groups of PVX are groups 1 4 (Cockerham, 1955). The other PVX stain is the resistance-breaking strain PVX^{HB} (Moreira *et al.,* 1980) and the more recently described PVX^{OS} (Kagiwada *et al.,* 2002) and PVX^{Tula} (Ravine *et al.,* 2008). The virus is transmitted mechanically from infected tubers (not by an insect vector)(Salazar, 1996). Plants often do not exhibit symptoms, but the virus can cause symptoms of chlorosis, mosaic, decreased leaf size, and necrotic lesions in tubers (Salazar, 1996). PVX can interact with PVY and PVA to cause more severe symptoms and yield loss than either virus alone (Jayashige *et al.,* 1989).

Types of potato virus resistance: Resistance to potato viruses is classified into extreme resistance (immunity), hypersensitive resistance (HR), resistance to virus movement, tolerance, resistance to infection and moderate resistance according to the

durability of each of the types of resistance (Solomon and Barker, 2001). Among the types of potato virus resistance, extreme resistance and HR are considered the most durable types of resistance. When a potato plant with genes for extreme resistance is innoculated with PVY or PVX, only extremely low amounts of viruses are detected using sensitive techniques (Solomon and Barker, 2001). Hypersensitive resistance is type of resistance that limits spread within the plant following the initial infection (Barker, 1987). This occurs when there is a lower percentage of a virus-infected daughter tuber from an infected plant resulting from impeded virus movement (Hutton and Brock, 1953). Tolerance is when there is little or no apparent effect on the infected plant especially when infected plants are symptomless or have reduced symptom expression in the presence of disease (Cooper and Jones, 1983). Resistance to infection or field resistance occurs when the likelihood of infection by natural means (i.e. from vector inoculation) is reduced in resistant plants (Cooper and Jones, 1983). This type of resistance is also manifested in plants that are resistant or unattractive to the vector itself (Flanders *et al.,* 1992). Moderate resistance refers to when the plants can be infected with the virus but virus accumulation in the plant reaches only relatively low concentration in the plant (Valkonen *et al.,* 1996).

Sources of virus resistance used for breeding for PVY and PVX resistance: Recognition of potato viruses as a serious problem in potato production in 1930's triggered a lot of research on the characterization of numerous virus resistance genes and phenotypes in *Solanum* species (Salaman, 1938; Cockerham, 1970; Solomon and Barker, 2001; Rahman *et al.,* 2010). Before recognition of this virus problem, selection for virus resistance within the *tuberosum* gene pool was done by selecting cultivars that were able to withstand virus degeneration better than others (Cockerham, 1943). Extreme resistance to PVY and PVX is found mainly in breeding lines and in wild species (Solomon, 1978). The existing cultivars and improved breeders' clones sometimes contain multiple copies of resistance genes or in other cases have different virus resistances combined (Solomon, 1998). The virus resistance genes are also available in wild species existing in various collections around the world (Barker, 1996). In many breeding programmes, a lot of emphasis has been put on identification, selection and utilization of extreme resistance to PVY and PVX than on other sources of resistance (Solomon and Barker, 2001). This is because selection for this type of resistance is relatively straightforward and can be carried out in the glasshouse following simple mechanical inoculation tests. Extreme resistance is also effective, quite durable and simply inherited and therefore easy to transfer to a desirable background (Solomon and Barker, 2001).

Introgression of PVY and PVX resistance genes to potato cultivars: Attempts by breeders to introgress PVY resistance started from about 1952 while introgressionPVX extreme resistance started from 1944 (Ross, 1986). This was after identification of the comprehensive nature of the Ry (for PVY resistance) and Rx (for PVX resistance) genes (Solomon and Barker, 2001). The Rx genes for PVX resistance and Ry genes for PVY resistance were originally found in S. *tuberosum ssp, andigena, S. acuale* and, *S. stoloniferum* respectively and then introgressed into the cultivated *S. tuberosum* gene pool (Solomon and Barker, 2001).

Introgression usually involves hybridization of the wild *Solanum* donor species with the cultivated *Solanum tuberosum* species, followed by repeated backcrossing and selection for the desired genotypes. However, not all potato species intercross freely because they differ in ploidy and endosperm balance number (Bradshaw and Mackay, 1994). This has posed problems for the introgression of resistance genes from host species. Solutions to these problems have been through bridging crosses and ploidy manipulation using intermediate species. These methods have been used to introgress resistance to PLRV, PVY and PVX from the non-tuberous *S. brevidens* into a *S. tuberosum* background (Ehlenfeldt and Hanneman, 1984) and PLRV resistance from the non-tuberous *S. tuberosum* into a tuber-bearing *Solanum* gene pool (Hermsen *et al.,* 1981). As a link between diploid and tetraploid species, the diploid *S. sparsipilum* has been used for introducing virus resistance (Cockerham, 1970). This approach is however time consuming and demands a lot of resources and is limited in genetic efficiency (Hermsen, 1981).

General potato breeding procedure: The general scheme for variety development in a complete breeding program involves raising the cross progeny in a glasshouse to produce the first clonal generation which can also be transplanted directly to the field when aphid populations are low (Solomon and Barker, 2001).

This is followed by planting single hill tuber families, observation plots (two seasons), replicated trials (four

seasons at different levels) and finally seed multiplication and naming of a variety.

This may take a period of 10-15 years (Bradshaw and Mackay, 1994).

Controlled pollination and production of hybrids: Controlled pollination in potato is an easy activity because the anthers are large and easy to remove and because pollen grains do not dehisce before or soon after flower opens (Simmonds, 1963). Plants grown in glasshouses need not to be bagged because the pollen is not easily distributed by wind (Caligari, 1992). The ovary starts swelling soon after pollination making it easy to identify a successful pollination (Simmonds, 1963). In the field, berries that develop from successful pollination can easily be bagged as they ripen on the plant. Open flowers are not selected for making crosses because of possible natural cross or self-pollination. The true seed from the berries produce seedlings that can be subjected to screening for disease resistance (Accantino and Malagamba, 1982).

Sometimes it may be difficult to obtain successful crosses because some clones or varieties do not normally flower at all (Pallais *et al.,* 1984) and in other cases, the pollen or the ovule may be sterile (Swaminathan and Howard, 1953; Ross, 1986). Different methods are used to induce flowering and to promote seed set. The daughter tubers are removed as they develop (Thijn, 1954) or the flower is decapitated and the stem is placed in a jar of water often with an antibacterial agent to reduce contamination (Peloquin and Hougas, 1959). The most common method of inducing flowering is grafting potato stems onto tomato stocks (Ross, 1986).

Preliminary screening of the viruses in greenhouses: Breeding for resistance to PVY and PVX involves evaluation of large numbers of hybrid cross progenies (Wiersema, 1972). Therefore it is important to eliminate maximum numbers of susceptible progenies as early as possible (Enrique and Fernandez, 1991). This is because field screening for virus resistance is expensive and therefore substantial cost savings can be made if satisfactory preliminary tests are carried out on glasshouse-grown plants (Cockerham, 1970).

Since PVY and PVX are manually transmissible, plants grown in glasshouses are inoculated with infected leaf extracts and the response observed over the following weeks (Wiersema, 1972).

Mass inoculation using spray gun has been the most effective and most commonly used methodof inoculating the largest number of seedlings within the shortest time possible (Solomon, 1978).

Spray gun method unlike manual inoculation of individual plants is known for its efficiency (10-20 times greater) in saving labor and time while reducing injury to the plant tissues during inoculation (Lindner and Kirkpatrick, 1959). The method also allows effective wounding, entrance of virus particles to the cell and fast healing (CIP, 1979). With this method, more than96 % of the seedlings are infected out of which more than 88 % show symptoms making it unnecessary to do second manual inoculation (Enrique and Fernandez, 1991). This method was first developed in 1955 and has been used in major breeding programmes both in Europe and United States of America (CIP, 1979). The method has also been used on different crops such as tobacco, wheat, oats, beans, cucumber and corn (CIP, 1979).

After successful inoculation, necrotic and mosaic symptoms are recorded and inoculated leaves tested for infection using serological or biological methods (Cockerham, 1970). Susceptible seedlings are discarded from about two weeks after inoculation (Wiersema, 1972). The immunity levels of resistance to PVY and PVX and the monogenic dominant inheritance facilitates the process of selection of resistant progenies. Resistant seedlings are then screened or evaluated in the greenhouse or in the field for other important pathogens like potato leaf roll virus (PLRV),late blight (*Phytphthora infestants*), *Altenaria solani* and nematodes (Jellis*et al.,* 1986).

Identification of parents for breeding PVY and PVX resistance: Progeny testing is done to determine the relative breeding value of parents or crosses and the gene dosage in a resistant parent or to select the best progenies (Solomon and Mackay, 1993).

This type of screening is carried out on glasshouse-grown plants to determine the number of copies of a major gene for resistance to PVY or PVX in a potato clone (Song *et al.,* 1991). The extreme resistant genotype is test-crossed with a susceptible parent and a sample of each progeny is sown and then spray-inoculated (Dhiman, 1994). The gene dosage in the resistant parent is deduced from the segregation ratio of resistant to susceptible seedlings in the progeny (Song *et al.,* 1991; Solomon and Mackay, 1993). Quadruplex (AAAA) parents have four (highest number of the single dominant PVY or

PVX resistance genes) followed by triplex (AAAa), duplex (AAaa), simplex (Aaaa) and then nulliplex (aaaa) without any copy of the dominant genes (Wastie *et al.* 1992). Multiplex parents meaning triplex or quadruplex with highest dosage of single dominant resistance genes (three or four copies) are most suitable for breeding PVY and PVX resistance (Wastie *et al.,* 1992; Bradshaw and Mackay, 1994). When such a parent is crossed with a susceptible cultivar, all the progeny, or (in the triplex case) nearly all, will be resistant reducing the cost and labour of preliminary screening and also makes it easy to combine virus resistance with other desirable characteristics (Cadman, 1942; Mendoza *et al.,*1996).

Parents with multiplex PVY and PVX resistance are produced through cycles of crossing, test-crossing and progeny tests to increase the number of copies of resistance genes in an individual clone (Mendoza *et al.,* 1996; Solomon, 1978). The resistant plants are then subjected to field testing.

Field-testing for PVY and PVX resistance: The purpose of field-testing is to expose the plants to natural conditions to determine level of virus resistance and to be sure that the results obtained are relevant to the real crop situation (Davies *et al.,* 1975). Field exposure is necessary for assessing quantitative field resistance toPVY and PVX and also useful for confirming the resistance of clones already selected for major gene resistance (Solomon, 1978). Field trials are grown in areas of high natural aphid infestation, but are more successful in some years than others, because the levels of aphid infestations do vary (Chandla *et al.,* 2001). Most clones with extreme resistance genes to PVY remain healthy infield exposure conditions or with a low frequency of infection (Davies *et al.,* 1975; Solomon, 1978; Solomon and Barker, 2001). The field trial exposes the plants to aphid virus vectors (predominantly *Myzus persicae*). Frequency of secondary infection in tuber progeny plants is assessed by symptoms, ELISA or a combination of the two, in comparison with standard cultivars (Davidson, 1973; Solomon and Barker, 2001). ELISA is one of the most sensitive serological techniques of potato virus detection (Hinostroza, 1981; Salazar, 1996). Virus detection using this technique is based on the ability of specific antibodies to react *in vitro* with their antigens (virus particles). More than one virus can be detected simultaneously by mixing the antibodies.

In Kenya, after seasons of evaluations and identification novel characters in new genotypes, local breeders forward successful genotypes to the Kenya Plant Health inspectorate service

(KEPHIS) for the national performance trials (NPT) normally conducted in at least six different agro ecological zones of potato growing in the country and over at least two potato growing seasons simulating future growing conditions of the crop (Lung'aho *et al.,*2006; Onditi *et al.,*2011). Released varieties are usually accepted by farmers and consumers depending on the number of multiple characteristics satisfying different consumers across the potato value chain (Kaguongo *et al.,* 2008).

Conclusion and recommendations: In choosing the appropriate starting point for breeding for durable resistance to PVY and PVX, traditional conventional procedures appear simple and straight forward and can still to be adopted by upcoming amateur breeders in Kenya due to the simple nature of genes involved. Conventional breeding for PVY and PVX can make significant contribution in improving local varieties in the national potato research programme where the modern molecular approaches of breeding have not yet established. Parents for breeding for resistance to the two viruses are available in both wild cultivated varieties available in major breeding programmes around the world and can be sourced to be used as parents by the national breeding programme. Field tested promising genotypes with additional market demanded characteristics will be useful in minimizing virus related crop losses. With virus resistant varieties, smallholder farmers who can not afford the pesticides and certified seed tubers would be able to grow their crop over a longer period of time without experiencing significant yield reduction over seasons.

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