

Improving Seed Health and Seed Performance by Positive Selection in Three Kenyan Potato Varieties

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Abstract Selecting seed potatoes from healthy-looking mother plants (positive selection) was compared with common Kenyan farmer practice of selection from the harvested bulk of potatoes (farmer selection) in 23 farmer-managed trials. Positive selection assured lower incidences of PLRV (39%), PVY (35%) and PVX (35%). Positive selection outyielded farmer selection irrespective of the agro-ecology, crop management, soil fertility, variety and quality of the starter seed, with an overall average of 30%. Regression analysis showed a relation between lower virus incidence and higher yield for the varieties. The paper discusses the consequences for seed system management in African countries. Furthermore possible additional effects of positive selection are discussed and further research is suggested. The paper concludes that positive selection can benefit all smallholder potato producers who at some stage select seed potatoes from their own fields, and should thus be incorporated routinely in agricultural extension efforts.

Resumen Se compararon las selecciones de papa-semilla de plantas donadoras aparentemente sanas (selección positiva) con la práctica común de selección por el productor Keniano del grupo de papas cosechadas a granel (selección

del agricultor) en 23 ensayos manejados por los productores. La selección positiva aseguró incidencias mas bajas de PLRV (39%), PVY (35%) y PVX (35%). La selección positiva superó en rendimiento a la selección del agricultor independientemente de la agro-ecología, manejo del cultivo, fertilidad del suelo, variedad, y calidad de la semilla original, con un porcentaje general de 30%. El análisis de regresión demostró una relación entre incidencia viral más baja y rendimiento más alto para las variedades. Este artículo discute las consecuencias del manejo del sistema de semillas en países africanos. Posteriormente se discuten los posibles efectos adicionales de la selección positiva y la sugerencia de más investigación. El artículo concluye que la selección positiva puede beneficiar a todos los productores pequeños de papa que en alguna etapa seleccionen papa-semilla de sus propios campos, y podrían así ser incorporados rutinariamente en los esfuerzos de la extensión agrícola.

Keywords Positive selection · Kenya · Potato · PVY · PVX · PLRV · Seed potato system · *Solanum tuberosum* · Virus

Introduction

The most important yield determining factor in potato cultivation is the quality of the seed tubers used (Lutaladio et al. 2009; Struik and Wiersema 1999). The difficult availability of affordable high-quality seed potatoes is the major constraint for potato production systems worldwide (Lutaladio et al. 2009; Struik and Wiersema 1999). Similarly, in East Africa the availability of affordable quality seed potatoes is a major obstacle for improving the profitability of potato production (Gildemacher et al. 2009b; Hirpa et al. 2010). The main factors reducing seed quality are biotic, including seed-borne viruses, bacteria and fungi, with a major component being the viruses (Salazar 1996).

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Positive seed potato selection is a simple practice to manage seed potato quality. It consists of selecting healthy-looking, vigorous mother plants to obtain seed tubers for the next seasons' crop. Positive selection has been proven to be a promising complementary practice for smallholder farmers in Kenya, in addition to seed production and marketing by specialized seed growers (Gildemacher et al. 2011). Specifically the fact that it has the potential to increase smallholder yields without monetary investment (Gildemacher et al., 2012a), and that it fits well into the prevailing seed sourcing strategy of smallholders, which is largely based on self- and neighbor supply (Gildemacher et al. 2009a) makes it a valuable complementary practice.

In earlier work (Gildemacher et al. 2011), a reduction in virus infection has been suggested as the main cause of yield increases by positive selection. This statement was supported by significant reduction in farmer-scored visual virus observations in farmer-managed demonstration trials, with no replications. The promising results have led to the incorporation of the practice as a component in seed system improvement interventions in Sub Sahara Africa (Gildemacher et al. 2012). Considering this promotion of the practice through agricultural extension, it was deemed appropriate to further investigate the effect of positive selection on virus incidence in potato plant populations.

In this paper data is presented from replicated researcher managed and farmer managed trials comparing positive selection with seed recycling, which is the common farmer practice in Kenya (Gildemacher et al. 2009a). Virus incidence levels were scored through DAS-Elisa. This paper investigates the effect of positive selection on yield and virus incidence, and analyses the relation between virus incidence and yield. The paper discusses the proven and possible additional causes of the yield effect of positive selection, and provides suggestions for the direction of future research to optimize the use of the simple practice of positive selection in seed potato system improvement in Sub Sahara Africa.

Materials and Methods

Source Fields and Starting Material

Seed tuber lots were purposely planted for the experiments described in this paper. Seed potatoes were sourced from four different types of sources: 1) basic seed from KARI-Tigoni-3 field generations; 2) certified seed from ADC Molo-6 field generations; 3) potatoes sold as seed in rural markets – unknown number of generations; 4) farmer saved seed – unknown number of generations. Three different varieties were sourced: Dutch Robijn, Tigoni (CIP 381381.13) and Asante (CIP 381381.20). This resulted in

a total of 23 different seed fields, planted without replication in a total of 15 locations.

Each of the 23 source fields was divided into two. From half the field, tubers were sourced by practicing positive selection, while on the other half of the field common farmer practice was applied. Positive selection entailed pegging healthy looking mother plants before full flowering by farmer groups which had received a basic group-based training (Gildemacher et al. 2007a). Just before full flowering virus infection symptoms are well visible. Two to four weeks after pegging the health status of the pegged plants was checked and pegs of plant showing newly developed systems removed. At harvest, pegged plants were harvested individually and seed sized tubers were collected to serve as seed tubers, provided all tubers of the individual plant looked healthy. Farmer selection consisted of the selection of seed sized tubers from the bulk of harvest potatoes from the other half of the source field, following common farmer practice.

Replicated Farmer Managed On-Farm Trials

The 23 sets of positive selection and farmer selection seeds were used to plant replicated farmer managed field trials at the same 15 different locations in the main potato growing areas of Kenya to compare the yields from the different types of seed tubers. Trials were planted either during the short rainy seasons (October'09–January'10) or the long rainy season (April'10–August'10), in a randomized complete block design (RCBD) layout with 3 or 4 replications of 40 plants each, at 30 cm × 75 cm distance.

Fertilization was based on 90 kg N/ha supplied in the form of NPK 10:26:10 at planting in the planting hole. Late blight was controlled through a spraying regime with Ridomil and Mancozeb, adapted in response to actual disease occurrence. Further management was done according to farmer practice. At harvest all marketable tubers (>30 mm) were collected and weighed.

For various reasons, e.g. porcupine damage, improper late-blight management or theft, not all 23 farmer managed experiments were successful. In total 21 data sets were obtained to reliably assess yield.

The pair-wise yield data was analyzed by testing for a significant difference between positive selection and farmer selection using a 1-tailed *t*-test.

Virus Infection Level Testing

From the seed selected through positive selection and farmer selection random samples of 40 tubers were taken to assess virus infection, from 20 of the 23 trials. Plants were grown from eyes cut from the individual tubers and planted in aphid-free greenhouse chambers. After 4–6 weeks leaf sap was obtained from these plants (Casper and Meyer 1981; Torrance

1992). Leaf sap samples were tested individually for infection with PVY, PLRV and PVX through enzyme-linked immunosorbent assay (DAS-ELISA: CIP, Lima, Peru).

The pair-wise virus infection data (expressed in % for the individual viruses tested) and yield data were analyzed by testing for a significant difference between positive selection and farmer selection using 1-tailed *t*-tests. Virus infection levels of PLRV, PVY and PVX were plotted against yield and trend lines were fitted using the SPSS curve estimation procedure (IBM SPSS statistics 20). In addition a combined virus infection indicator was calculated by taking the simple absolute sum of the number of infected sample tubers in the total sample of 40 tubers per treatment. This index can be larger than the total number of tubers in the sample and should be considered as a measure for the virus load. For this index the same plotting procedure was used.

Replicated On-Station Factorial Fertilizer × Seed Source Trials

An additional replicated factorial trial, with the varieties Asante, Tigoni and “Purple Tigoni”, a landrace, was planted under researcher control to test for fertilizer × seed selection interaction during the long rainy season of 2010. The trial was planted in a split-plot layout with fertilizer treatments as main plots and selection method × variety as subplots. The seed was sourced from four ware potato farmer groups involved in the on-farm trials described above. Two fertilizer levels were implemented using NPK 10:26:10 at 45 and 90 kg/haN equivalent. Each plot counted 40 tubers at 30 cm within-row and 75 cm between-row distance. At harvest all marketable tubers (>30 mm) were collected, weighed and counted. Data were analyzed with ANOVA and protected LSD values were assessed.

Results

The results from a total of 18 farmer managed randomized complete block trials are summarized in Table 1. When analyzing the combined paired observations through a *t*-test, positive selection clearly out-yielded the farmer selection treatment, irrespective of variety or quality of the starter material.

For all three varieties, positive selection resulted in substantially higher yields, the difference ranging from an average of 23% for Tigoni to 35% for Dutch Robijn. The average absolute yield increase for high-quality starting material was 7.3 t/ha, whereas farmer-quality starter material gave an average yield increase of 3.0 t/ha.

Table 2 shows the summarized results of the researcher-controlled replicated trials implemented with seed potatoes sourced through positive selection and through farmer

selection. Two different fertilizer regimes were implemented to assess the interaction with the effect of positive selection. There was no interaction between fertilizer level and the effect of positive selection. A higher fertilizer level did increase significantly both yield and the number of tubers harvested. Positive selection increased the average yield to 13.4 t/ha as compared with 10.6 t/ha for using farmer selection seed potatoes. This constitutes a 26% increase in yield. The number of tubers harvested increased by 23%, from 21.9 to 26.8 m⁻².

Table 3 shows the average effect of positive selection compared with farmer selection on PLRV, PVY and PVX infection rates as measured through DAS Elisa testing. The results show a significant reduction in PLRV, PVY and PVX infection rates. The average measured PVY infection was 25.0% after positive selection, compared with 38.4% for farmer selection. The infection rate with PLRV went down from 31.1% for farmer selection to 19% for positive selection. At the same time yields increased by an average 25.6% as a result of positive selection.

The yield differences observed in the individual trials were plotted against the in virus infection rate (Fig. 1). For Tigoni and to a somewhat lesser extent Dutch Robijn the expected negative correlation between yield and virus levels was observed. The variety Asante did not respond significantly to a reduction in infection with PVY and PVX, and responded less than the other two varieties (but significantly so) to a reduction in PLRV. When plotting tuber yield against the sum of the number of infected tubers in each sample (assessed through growing plants from eye-cuttings and testing virus infection in a leaf sample) for the three viruses, this could account for 70% and 46% of the variation for Tigoni and Dutch Robijn, respectively, while for Asante it could only account for 17% of the variation.

Discussion

Positive Selection Results in Yield Increase Compared with Farmer Selection

The results from the trials confirm the earlier findings from farmer managed demonstration trials (Gildemacher et al. 2011; Gildemacher et al., 2012a) that positive selection is a practice that can provide smallholder producers with a significant yield advantage compared with the common practice of indiscriminate recycling of seed potatoes from their ware potato harvest. For three different popular Kenyan potato varieties over a wide range of agro-ecologies and (farmer) management practices (Table 1), for two levels of fertilizer application (Table 2) and for different qualities of primary material (Table 1), the simple practice of selecting the best looking plants as a seed source for next season's crop gave a highly significant yield advantage under all

Table 1 Yield from positive seed potato selection compared with common farmer seed potato selection presented separately for the varieties Asante, Tigoni and Dutch Robijn, and for two quality levels of the source field

Name	Yield ^a				Yield increase				
	PS (t/ha)	Std. Dev.	FS (t/ha)	Std. Dev.	(t/ha)	%	t-value	df	p (2-tailed)
Asante	13.9	1.97	11.0	2.20	2.8	25	7.49	21	0.000
Tigoni	18.6	7.37	15.1	5.99	3.5	23	3.75	19	0.001
Dutch Robijn	20.9	10.13	15.5	6.93	5.4	35	6.31	25	0.000
Farmer quality ^b	14.1	2.31	11.1	2.11	3.0	27	4.84	51	0.000
High quality ^c	30.5	6.99	23.1	4.19	7.3	32	13.36	15	0.000
All	17.9	8.00	13.9	5.80	4.0	30	14.38	67	0.000

^a PS positive selection; FS farmer selection

^b Seed potatoes for these trials selected from fields planted with seed potatoes from local market or farmer fields

^c Seed potatoes for these trials selected from fields planted with basic seed or certified seed

tested circumstances over just selecting from the bulk of the harvest, as farmers tend to do (Gildemacher et al. 2009a).

The three different varieties appeared to differ in their reaction to positive selection, with Dutch Robijn responding most strongly with an average yield advantage of positive selection over common farmer practice of 5.4 t/ha, or 35%, whereas for Tigoni and Asante varieties a yield increase of 23 and 25% was recorded on average (Table 1).

The farmer managed trials showed that positive selection is an effective practice for seed potato populations of different generations. Positive selection resulted in substantial yield increases when used to source seed potatoes from farmer ware potato plots, but it also increased yields when applied on fields planted with relatively high-quality seed potatoes from certified seed potatoes (6 generations of multiplication) and basic seed potatoes (3 generations of multiplication) (Table 1).

Table 2 Effect of seed selection method under two different fertilizer regimes (45 or 90 kg N per ha based on NPK 10-26-10) on yield (t/ha) and number of tubers (#/m²), Kabete, Nairobi, Kenya, 2010

Fertilizer regime and seed selection method	Yield ^a (t/ha)	No. tubers ^b (#/m ²)
45 kg N/ha		
Positive selection	11.7	23.8
Farmer selection	8.9	18.7
Total	10.3	21.3
90 kg N/ha		
Positive selection	15.0	29.8
Farmer selection	12.4	25.0
Total	13.7	27.4

^a No significant interaction between fertilizer level and selection method (F pr.=0.698). All yield contrasts significantly different, LSD 5%=0.49

^b No significant interaction between fertilizer level and selection method (F pr.=0.759). All yield contrasts significantly different, LSD 5%=1.30

It is in itself not surprising that the practice works, as it has been in use in clonal selection in the first stages of conventional seed potato multiplication (Salazar 1996; Struik and Wiersema 1999). The Canadian seed potato system even has a specific directive describing the accepted procedure to source starter material for pre-elite seed production from ordinary potato fields through positive selection (Canadian Food Inspection Agency 2010). However, what is more important is that also ware potato producers are able to learn and implement the practice successfully (Bryan 1983) and substantially increase their productivity compared with their common practice of selecting seed potatoes from the bulk of the harvested tubers.

Positive Selection Reduces Virus Infection Compared with Farmer Practice

Explaining the convincingly demonstrated yield increases is however more complicated. The combined results of the farmer managed and researcher managed trials demonstrated that positive selection had a strong effect on the measured virus infection rate of seed tubers selected through positive selection compared to seed tubers selected from the bulk of the harvest (Table 3; Fig. 1). PVY and PLRV infection rates measured in the farmer selection seed were above 30%, while in the positive selection treatment the infection rate was reduced by 35 and 39%, respectively (Table 3). The measured rates of infection for PVX in farmer selection was lower at 7.5%, but also PVX levels were reduced after positive selection as compared with farmer selection (Table 3). Even under the high disease pressure prevailing in farmer managed fields with potatoes that were recycled for several generations, substantial reductions were measured in the infection rates of the selected tubers. This shows that positive selection, practiced by smallholder ware potato producers is a powerful practice to keep virus infection levels in check.

Table 3 Effect of positive selection compared with farmer selection on the level of infection with potato viruses PLRV, PVX and PVY and progeny yield (t/ha) of selected seed tubers

	Farmer selection (FS)		Positive selection (PS)		Difference PS-FS			
	Infection rate (%)	Std. dev.	Infection rate (%)	Std. dev.	Infection rate (%)	Relative change (%)	t value (df=20)	P (1-tailed)
PLRV	31.1	14.15	19.0	8.17	-12.1	39.0	7.00	0.0000
PVX	7.5	6.54	4.9	4.55	-2.6	35.0	2.93	0.0043
PVY	38.4	18.40	25.0	12.57	-13.4	34.9	8.06	0.0000
	Yield (t/ha)	Std. dev.	Yield (t/ha)	Std. dev.	Yield (t/ha)	Relative change (%)	t value (df=20)	P (1-tailed)
Tuber fresh yield	12.90	4.72	16.21	5.81	3.31	25.6	7.72	0.0000

The Relationship Between Yield Increase and Virus Reduction

Both yield increases and a reduction in virus infection could be demonstrated beyond any doubt in a very wide variety of

circumstances. In addition the data show a significant correlation between yield and virus infections (Fig. 1), suggesting that an important mechanism behind the effect of positive selection is the reduction in virus infection in the plant population.

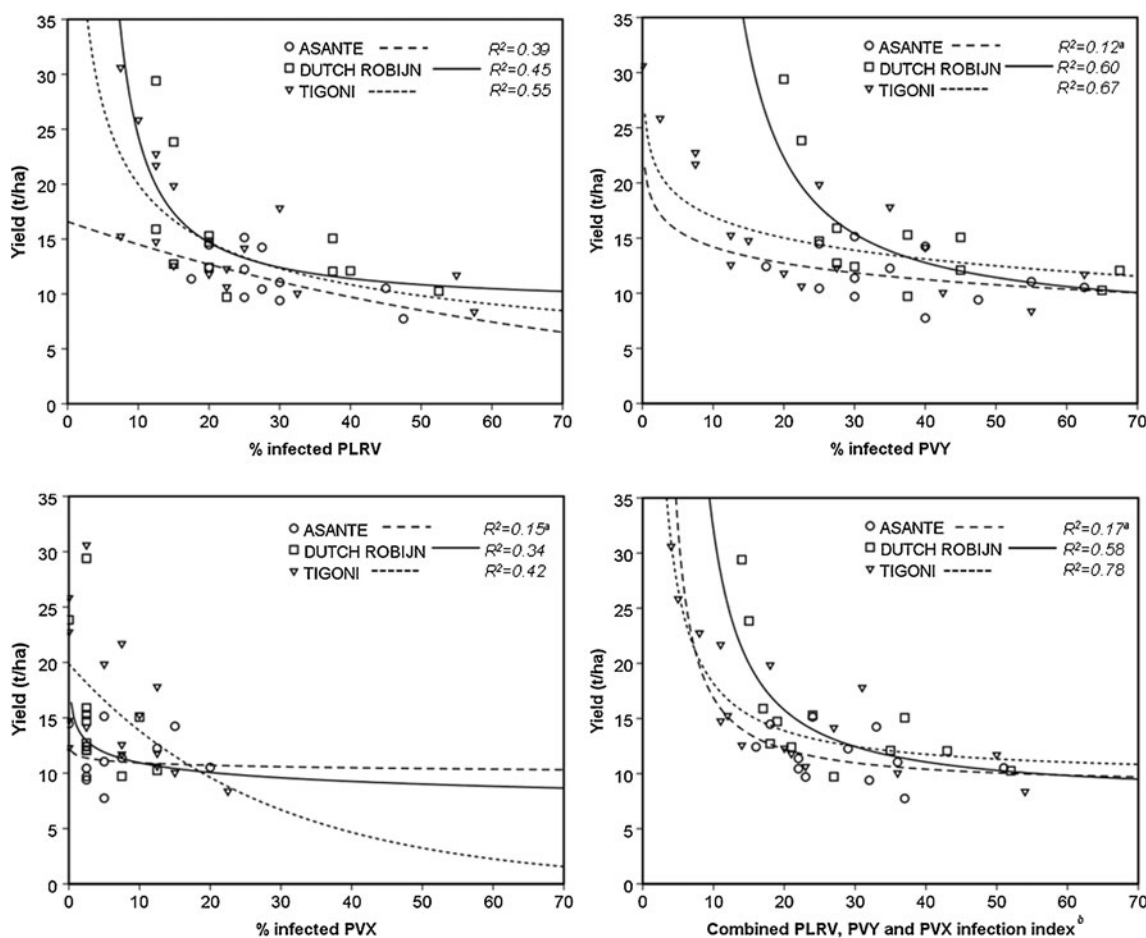


Fig. 1 Fresh tuber yield (“Yield”) plotted against the percentage infection with PVY, PVX or PLRV and against the sum of the infection count of all three viruses for the potato varieties Asante, Dutch Robijn and Tigon. ^a ns = non significant regression ^b index calculated as the

simple absolute sum of the number of infected tubers for each virus in the total sample of 40 tubers. This index can be larger than the total number of tubers in the sample and should be considered as a measure for the virus load

For Tigoni and Dutch Robijn, a similar response can be observed (Fig. 1). Lower yields were obtained when infection rates were higher. The figure demonstrates graphically that in the trials in which higher yields were obtained, an increase in virus incidence was of more consequence compared to the trials in which low yields were obtained. This is in line with the observation in Table 1 that positive selection gives high yield increases when applied on fairly high-quality seed.

The correlation between PLRV, PVY and PVX infection and yield of Tigoni and Dutch Robijn is significant with respectively 12 and 16 data points (Fig. 1) under highly heterogeneous circumstances. Seed potatoes were derived from different sources with widely different history in terms of number of generations of multiplication and crop management. In addition the trials were planted under different circumstances across Kenya, with as a consequence different virus pressure. Finally the actual positive selection was done by different groups of producers. Still, a convincing correlation could be demonstrated between virus infection rates and yield.

The shape of the relationship between virus infection and yield is different from what could be expected based on work by Reestman, who predicts an S-shaped curve, with limited effects of virus infection at lower incidences, and a diminishing effect at very high incidences (Reestman 1946; Reestman 1970), based on the compensation effect. Van der Zaag (1987) calculated that further increasing virus incidence would have stronger yield consequences in an already highly infected crop compared to a lightly infected crop. It is mentioned by Reestman (1970) that the yield reducing effects mentioned across the literature of that time are diverse and confusing, and he suggested that this depended on the rate of compensation by neighboring plants. Low fertility, drought and few stems per plant were mentioned as factors impeding compensation. All these three factors are very common in smallholder potato production in Kenya. Potato virus infection may well do more damage under these sub-optimal growth conditions than under more favorable conditions. Furthermore infection rates under which virus effects were observed to be largely compensated by neighboring healthy plants were low (<10%) (Reestman 1970). Authors agree that damage can become more severe as the result of multiple infections with different viruses, a situation common in Kenya (Gildemacher et al. 2009a; Radcliffe and Ragsdale 2002).

Possible Additional Mechanisms Contributing to the Effect of Positive Selection

The variety Asante only showed a significant yield response to a reduction in PLRV infection, but less pronounced than the varieties Tigoni and Dutch Robijn. In addition Asante showed no response to a reduction in PVY or PVX. This

suggests that Asante harbors partial resistance or tolerance for these viruses. Differences in response to virus infection between varieties are common (Bawden et al. 1948; De Bokx 1972; MacKinnon and Munro 1959; Radcliffe and Ragsdale 2002). In the case of extreme resistance however, the virus would not be detected through DAS-ELISA.

The yield response of Asante to positive selection was similar as for the other two varieties, while it does respond much less strongly to a reduction in PVY, PLRV and PVX incidence. This suggests that in addition to a lower incidence of PLRV, PVY and PVX, there might have been other factors that played a role in the measured effects on yield resulting from positive selection.

The most likely explanation is that other viruses which were not tested have also been reduced in incidence as a result of positive selection. PVM and PVS were found to be abundant in farmer based seed systems in Kenya (Muthomi et al. 2009), while PVA was found to be common in seed tubers sold at Kenyan rural markets (Gildemacher et al. 2007b). PVA is often not considered to cause serious damage, but can cause severe symptoms in combination with PVY or PVX (Nganga and Shideler 1982), a common combination of infections in farmer fields in Kenya (Gildemacher et al. 2009a). Any endemic virus disease that would cause visible symptoms will be affected by positive selection, and would have contributed to the yield increase realized by positive selection compared with common farmer practice.

Synergistic effects of infection with multiple viruses have been described by several authors for different virus combinations of sweet potato (Karyeija et al. 2000; Untiveros et al. 2007), soybean (Malapi-Nelson et al. 2009), tomato (Balogun et al. 2005), wheat (Tatineni et al.), and numerous other crops. In case of synergistic effects between viruses on potato yield, this may further increase the influence of a reduction in virus incidence of those viruses not detected here. Synergistic effects between PLRV and both PVY and PVX were demonstrated for susceptible potato varieties (Brandolini et al. 1992).

Similarly to virus infection levels, the levels of other seed borne diseases having an effect on general plant appearance will be affected by positive selection. Turkensteen (1987) identified *Erwinia* spp. bacteria (currently *Pectobacterium* spp.) and *Fusarium* spp. fungi as 'important' seed-borne pathogens in Central Africa. In addition bacterial wilt (*Ralstonia solanacearum*) is endemic in Kenya (Wakahi et al. 2007). For the latter however the symptoms can hardly be mistaken and all was done to avoid bacterial wilt infection of the trials.

In addition to having an effect on the incidence of viruses on the potato plant population, it cannot be ruled out that positive selection results in a lower virus load of individual seed potatoes, the virus titer. Little is known about the effect of virus titer in seed tubers on the final yield. Van der Zaag (1987) reported that tubers infected late in the previous season had less severe

symptoms and yield reduction than those infected earlier and mentioned that diseased tubers that had been recycled for a number of generations did worse than those having a shorter history of infection. However, no data to support this were presented. Barker and Woodford (1987) reported unusually mild PLRV symptoms in the progeny of late-infected mother plants. Interesting enough however, they could not show a difference in virus titer in the leaves about 7 weeks after planting the progeny tubers. Satoh et al. (2011) do provide some evidence that the gene response and resulting symptom expressions of rice plants to infection with Rice Dwarf Virus (RDV) are related to the concentration of the virus in the plant. Further research to improve the understanding of the effect of positive selection on average potato crop virus titer, and the effect of virus titer on crop growth would be of interest.

Effect of Soil Fertility on Effectiveness of Positive Selection

Not surprisingly, potato yields increased with a higher fertilizer application. It could theoretically be expected that poorly nourished plants suffer more from the same level of virus infection, as has also been reported (De Bokx and Van de Want 1987). Especially abundant nitrogen fertilizer can mask the visual mosaic symptoms of virus infection (Salazar 1996). On this basis it could be hypothesized that a poorly nourished crop would benefit more from positive selection than a well fertilized crop. However, under the fertilizer regimes tested no interaction between the effect of positive selection and soil fertility management could be observed.

Remaining Research Questions

The result from this research has conclusively shown that positive selection is a suitable practice for seed potato quality maintenance by smallholder potato producers. The viruses PVX, PVY and PLRV have shown to play a role, but it appears there may be additional factors, most likely other viruses and possibly other soil borne diseases, contributing to the effect of the practice. Targeted controlled research to investigate such additional factors would increase the understanding of the mechanisms behind positive selection.

A remaining topic of interest for further research is the development of the yield potential of potato crops under positive selection over several generations. Current seed potato system management decisions are based on the assumption that degeneration as a result of tuber-borne diseases is an inevitable fact, and that regular seed renewal from a reliable disease-free source is the only manner to maintain an acceptable yield potential. This research has shown that positive selection assists in managing virus infection levels. It would be of interest to witness potato

yields over several generations of applying positive selection to a degenerated potato crop. This would allow one to challenge the common belief that degeneration is inevitable and irreversible in a potato population. It could be hypothesized that opposed to degeneration of a potato plant population over generations, also regeneration needs to be considered an option, provided ware potato farmers manage their selection process well.

Answering this question is of great essence for seed potato systems in countries where production levels are, unlike in some developed countries, not close to the theoretically optimal production. A better understanding of the rate of degeneration in relation to disease pressure and farmer management will allow for better informed investments in seed potato program building and the seed renewal strategy by individual potato producers. Combined economic and seed degeneration research could contribute to this improved decision making.

Virus resistance and virus tolerance are elements requiring attention in further research. Genetic variation in virus resistance and tolerance has been identified and is used in breeding programs (Arif et al. 2011; Brandolini et al. 1992; Munro 1961). Combining virus resistance in popular potato varieties with better seed quality management by ware potato producers through positive selection may reduce the importance of commercial seed potato multiplication, which has proven to be difficult to establish in developing countries.

Before such far reaching conclusions can be made, however, further follow-up research to address the point above is needed. The authors would, in this regard, like to suggest a factorial trial with variety (1), starter seed infection (2), and seed quality management (3) as factors, to be continued over a minimum of four generations:

1. Variety
 - a. Fully susceptible variety
 - b. Best known resistant and tolerant variety
2. Starter seed infection
 - a. Tested and quantified highly virus infected seed potatoes
 - b. Tested and quantified very low virus infected seed potatoes
3. Seed quality management
 - a. Seed recycling with positive selection
 - b. Blind seed recycling (farmer selection)
 - c. Flush out by new seed multiplied from original starter seed each season

Virus infection levels would have to be monitored intensively to assure maximum understanding of the virus epidemiology, and especially the dynamics of virus epidemiology over generations, both in terms of the fractions of infected

plants and tubers, but also in terms of titer build-up in plants and tubers.

Such research is time and resource consuming and risk prone. Frequent observations need to be made and samples taken and investigated over a number of generations, which would call for trials, situated on research stations with reliable irrigation systems. However, to stay close to common practice, on-farm trials may be better suited, which would reduce researcher control and increase the risk of failure somewhere over the four generations.

Finally, as (Döring 2011) indicates, virus epidemiology is highly complex as a result of the numerous interactions between viruses, vectors, the plant and the environment. He observed that to detect meaningful patterns large amounts of data are needed, after which the question remains to what extent findings can be generalized. Still, a better understanding of how positive selection impacts on yield of potatoes would in our case be supportive to efforts to make this practice the standard for potato producers who have the habit to recycle seed from their last crop.

Consequences of the Research Findings

The research findings demonstrate conclusively that positive selection is a practice that works under very diverse circumstances. If potato producers decide to source seed potatoes from their previous crop, rather than renewing their seed from a reliable source of high-quality seed, positive selection is highly recommended.

Considering the highly conclusive results with regard to the effect of positive selection, and the fact that the practice requires only sticks or another type of marker and labor as input, it is very suitable for seed quality maintenance by smallholder potato farmers, who form the majority of potato farmers in Sub-Saharan Africa. Gildemacher et al. (2011) demonstrated that an average Kenyan potato producer who invests 4 mandays per hectare in positive selection can realize 284 Euro additional profit, after deducting 6 Euro opportunity cost for his labor investment. In addition positive seed potato selection can fairly easily be learned (Gildemacher et al. 2012b). Based on these findings it can be recommended to include positive selection in the training curricula and programs of smallholder potato farmers in countries where sourcing seed potatoes from their own ware potato crop is common practice.

It has to be emphasized that positive selection is not very suitable for commercial seed potato multiplication. For seed quality maintenance it would suffice to mark roughly 10–15% of the potato plants in a field as mother plants to source seeds for the next season for a same sized plot. A seed multiplier requires to bulk seed over seasons from a limited amount of starter seed, and thus requires harvesting the vast majority of

his plants as seed. For seed multiplication removing visibly infected plants, negative selection, remains the only option.

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