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Potato virus Y and *Potato leafroll virus* management under climate change in sub-Saharan Africa

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Potato has increased in importance as a staple food in sub-Saharan Africa, where its production is faced with a multitude of challenges, including plant disease development and spread under changing climatic conditions. The economically most important plant viruses affecting potatoes globally are *Potato virus Y* (PVY) and *Potato leafroll virus* (PLRV). Disease management relies mostly on the use of insecticides, cultural control and seed certification schemes. A major obstacle in many sub-Saharan Africa countries is the availability of disease-free quality seed potatoes. Establishment and implementation of quality control through specialised seed production systems and certification schemes is critical to improve seed potato quality and reduce PVY and PLRV sources. Seed could be further improved by breeding virus-resistant varieties adapted to different environmental conditions combined with management measures tailored for smallholder or commercial farmers to specific agricultural requirements. Innovative technologies – including more sensitive testing, remote sensing, machine learning and predictive models – provide new tools for the management of PVY and PLRV, but require support for adoption and implementation in sub-Saharan Africa.

Significance:

- *Potato virus Y* (PVY) and *Potato leafroll virus* (PLRV) are the two major potato viruses threatening profitable seed potato production.
- High-quality seed shortage in many sub-Saharan Africa countries has been identified as a constraint to increasing yield.
- Specialised seed grower or seed certification programmes should be implemented to prevent virus transmission from seed to daughter tubers.
- Sustainable PVY and PLRV management in seed potatoes requires specific regional approaches to growth, farming and climatic conditions.
- Future research should include predictive models and new innovative technologies such as more sensitive testing, machine learning and remote sensing.

Introduction

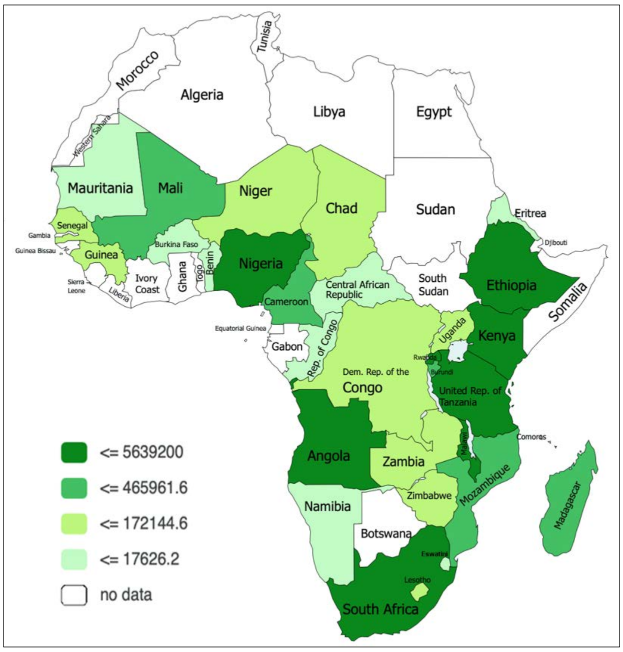
Potato (*Solanum tuberosum* L.; Solanaceae) is a high yielding cash crop in sub-Saharan Africa.[1] Its production has experienced one of the largest increases in comparison with other staple food crops in the region.[1] The potato production area more than doubled in sub-Saharan Africa between 1998 (655 447 ha) and 2018 (1.47 million ha), including in regions with high poverty rates, but yields vary greatly across the region (Figure 1).[2] However, food security in sub-Saharan Africa remains a chronic problem.[3] Although there is sufficient food to satisfy global average food consumption in lower-income countries, several countries in sub-Saharan Africa suffer from food insecurity due to low production with limited access to food produced in other countries.[4] Food security is likely to worsen with the impact of climate change and a growing population.[4] The effects of climate change are expected to be most severe in sub-Saharan Africa because of the high dependence on agriculture and its vulnerability to extreme weather events.[3,5]

Predicted climate change impact in sub-Saharan Africa is highly complex and region specific. Droughts and heat waves, unseasonal rainfall, and an increase in the frequency of extreme weather events are likely in future.[6,7] The climate in sub-Saharan Africa has already changed with mean increases in temperature from a 1951–1980 baseline to 2019 of 1.5 °C, ranging from 1.0 °C in South Sudan and Eritrea to 2.3 °C in Namibia.[2] Simultaneously, rainfall patterns have become even more variable with regional decreases in southern Africa and increases in eastern Africa.[7] This variability is exacerbated by erratic severe drought episodes.[8,9] Regional adaptations to maintain at least current yields in potato production in the increased area planted[10] are therefore crucial as most potatoes are grown under dry-land conditions during specific rainy seasons[11].

The impact of climate change on potatoes globally has been reviewed by Hijmans[12], Haverkort and Verhagen[13], Raymundo et al.[14] and George et al.[15] Little detailed information is available for sub-Saharan Africa. Simulation models for agro-ecosystems with continental and Mediterranean climates in South Africa suggest that increased CO_2 levels will impact positively on water use by potato plants and thus yield, compensating for negative effects of increased temperature and reduced water availability, provided crops are grown at suitable times.[16,17] However, potatoes grown under heat stress are likely to have a lower water use efficiency and reduced yields, even under increased CO_2 levels.[16,17] Changing climatic conditions could therefore reduce potato production in the lowlands in sub-Saharan Africa by up to 50% by 2050.[14] In eastern Africa, where potatoes are grown mainly in the highlands, heat and water stress have been predicted to reduce yield, with the exception of Rwanda.[18] Potato production regions in the Ethiopian Highlands, for example, are faced with a potential increase of 0.7 °C from 1975 to 2050.[19]

One of the major biotic limitations to potato production are plant diseases. Their impact may be even more severe in warmer regions where seed potato tubers are propagated over several generations, and year-round plantings are already under continuous pressure from insect-transmitted pathogens.[20] Furthermore, an increase in temperature or milder winters may have a negative effect on seed potato systems that rely on cooler growing regions or cool winters for reducing plant virus inoculum and low insect vector pressure.[20]

More than 50 plant viruses that infect potatoes have been recorded[20], of which two – *Potato virus Y* (PVY; genus *Potyvirus*, family Potyviridae) and *Potato leafroll virus* (PLRV; genus *Polerovirus*, family Luteoviridae) – affect profitable potato production globally[20,21]. PVY has overtaken PLRV as economically the most important of the potato viruses.[20] PVY has been a challenge worldwide during the past 20 years due to the emergence of recombinant PVY variants.[22,23] Both viruses result in dramatic yield and quality losses.[21,24] Infection levels are increased by planting infected tubers, leading to increased infection levels over successive generations. Thus, PVY or PLRV infection can lead to downgrading or rejection of seed lots if tolerance levels set by seed potato certification schemes are exceeded.[25-28] Tubers from informal seed systems, previous crops or tubers that are unmarketable are often used for planting[29]; this becomes a severe problem, especially for smallholder farmers in sub-Saharan Africa.



Source: ©FAO[2]

Figure 1: Potato production (in tonnes) in sub-Saharan Africa (mean 2014–2018).

Both PVY and PLRV are transmitted to the new potato crop through aphid (Hemiptera: Aphididae) vectors (horizontal transmission; primary infection) or via infected seed tubers to daughter tubers (vertical transmission; secondary infection). The severity of infection depends on host plant tolerance, time of infection (with early infection leading to higher yield loss), environmental factors and virus strains involved.[30,31] PVY and PLRV management relies largely on cultural preventative measures that limit virus inoculum or curative measures using insecticides to suppress aphid vector species.

Climate variability and climate change as well as agricultural changes (including introduction of new genotypes, germplasm movement and cultural intensification) add to the intricacy of the already complex virus–insect vector–plant–environment interactions.[32,33] The impact of climate change on plant viruses has been recently reviewed by Islam et al.[33], Jones[34,35], Jones and Naidu[36], and Trebicki[37].

The impact of climate change on aphid vector species and abundance is complex, difficult to predict and region specific[38-41] and depends on plant species, variety and age, and duration and severity of climate stressors and aphid species[42,43]

This review focuses on strategies to manage the spread of PVY and PLRV in potato crops in sub-Saharan Africa under changing climatic conditions. Research findings are reviewed and evaluated with specific reference to potato production in the sub-Saharan African context. Areas requiring further research to manage PVY and PLRV in sub-Saharan Africa are identified.

Potato virus Y

Potato virus Y (PVY) is a single-stranded RNA virus. Several strains have been identified – PVY^{O} (common strain), PVY^{N} (tobacco veinal necrosis strain), and PVY^{C} (stipple-streak strain, including potato virus C), and during the past two decades recombinant variants derived from PVY^{O} and PVY^{N} have become prevalent worldwide, e.g. PVY$^{N:O}$, PVY^{NTN} (N-tuber necrotic), and PVY$^{N\text{-}Wi}$ (N-Wilga).[22,23,44] PVY infection increases the number of undersized tubers. Foliar symptoms include mosaic (chlorotic patches; Figure 2a) that may be severe or mild and hardly detectable.[45] Mild symptoms cause problems for virus management in potato seed production because symptomless plants remain unidentified and therefore are not eliminated and serve as virus inoculum.[30] Some recombinant variants cause potato tuber necrotic ringspot disease (Figure 2b).[45]

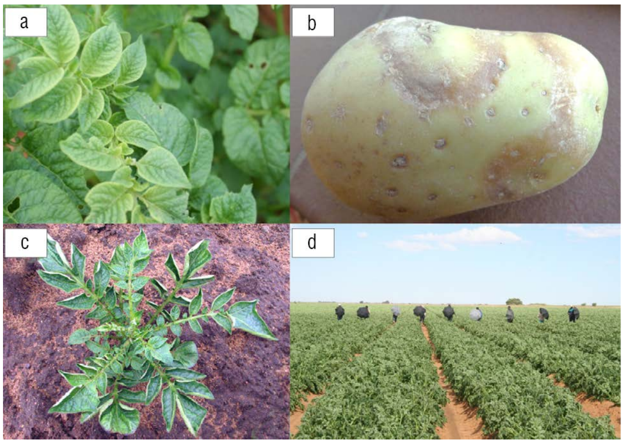


Figure 2: (a) Potato leaflets with mosaic (chlorotic patches) symptoms of *Potato virus Y* (PVY). (b) Potato tuber with necrotic lesions caused by PVY^{NTN} infection (photo: Potato Certification Service, South Africa). (c) Foliar symptoms of *Potato leafroll virus* (photo: Diedrich Visser, Agricultural Research Council – Vegetable and Ornamental Plants). (d) Roguing of plants expressing PVY symptoms in South Africa. Farm employees use umbrellas to facilitate the recognition of leaflets with mosaic symptoms.

PVY is primarily transmitted through aphid vectors, but can also be transmitted mechanically or by grafting but not through true seed.[31] PVY is transmitted non-persistently. The virus does not replicate in the vector and there is no latent period (time between virus acquisition and when a vector becomes infective). Aphid vector species acquire and transmit PVY to an uninfected plant during short feeding probes of seconds to minutes of epidermal cells. Aphids tend to lose the ability to transmit PVY after probing one or two uninfected plants or virus non-host plants. They can become infected again when feeding on an infected plant. PVY can be transmitted by 65 aphid species or species groups that either breed on potato (colonising species; e.g. *Myzus persicae,* the most efficient vector) or are transient species that land and probe or feed but do not breed on potato (non-colonising species; e.g. *Rhopalosiphum padi*).[30] Transient species, although less efficient in PVY transmission[30], are important because they may occur in high numbers. Therefore, both colonising and transient species are of importance when devising management strategies.[30]

PVY transmission and infection of plants is temperature dependent. High temperatures of 25–30 °C negatively influence virus transmission and virus titre at these temperatures decreases over time.[46] Whereas virus establishment in *Nicotiana benthamiana* (Solanaceae) was highest between 20 °C and 30 °C, the virus titre decreased over time in plants at 25 °C and 30 °C.[46]

Potato leafroll virus

Potato leafroll virus (PLRV) is a single-stranded RNA virus. Primary infection symptoms include upward rolling of the leaflets (Figure 2c), while secondary infection symptoms include stunting of shoots and upward rolling of leaflets.[21] Yield losses through stunting of plants and reduced tuber size and number are highest when planting infected tubers and through early infection of young virus-free plants by viruliferous aphids.[31] Apart from reducing yield, PLRV causes internal net necrosis of tubers of some cultivars, rendering them unsuitable for seed, marketing and processing.[20] Mature plants are less affected than young seedlings.[31]

PLRV is most commonly transmitted by aphids, and through grafting, but not mechanically nor through true seed.[31] The virus is transmitted through aphid vector species in a persistent, circulative, non-propagative manner, i.e. individuals remain infected for life (the virus is passed on through moults), but PLRV does not replicate in the vector and the virus is not passed on to offspring.[31] Vectors of PLRV must feed on the phloem sap of potato plants to acquire and transmit the virus. PLRV can be both acquired from infected plants and transmitted to healthy plants by aphid vectors with feeding times of 10–15 min but maximum virus acquisition occurs after feeding of approximately 12 h. Aphid vectors become infective after a latent period of 8–72 h.[31] To date, 13 potato-colonising aphid species or species groups have been identified as vectors.[47]

The highest titre of PLRV was recorded between 20 °C and 30 °C in *Physalis floridana* (Solanaceae).[46] The PLRV growth rate decreased from 25 °C and ceased at 35–40 °C, possibly due to gene silencing.[46,48]

PVY and PLRV management

Potato management, including disease management, requires an integrated approach and regional cooperation among growers.[10,31] Potato virus control worldwide is currently largely achieved through seed quality and certification, vector control with insecticides and cultural control methods.[28,31] Management of PVY poses an even greater challenge than that of PLRV, because it is transmitted non-persistently within seconds and insecticides may have a limited effect.[49] Effective PVY management relies therefore on prevention.[28] Depending on the prevalence of PVY or PLRV in a region and local conditions, a combination of various management strategies may be required for both viruses.

Climate change might affect commercial and smallholder farmers in different ways because of different production systems. In general, farmers may have to reassess current disease management practices. Apart from maximising soil and water conservation, integration of a variety of existing and innovative emerging strategies is likely to be required to cope with increasing uncertainty, and variable rainfall and temperatures.[10,50] General reviews of plant virus management strategies can be found in Jones and Naidu[36] and Kreuze et al.[20] Radcliffe and Ragsdale[31] and Dupuis et al.[28] reviewed management strategies for PVY and Radcliffe and Ragsdale[31] for PLRV. The following provides a brief overview of management options with emphasis on sub-Saharan Africa.

Seed quality and seed certification

The risk of PVY and PLRV spread can be minimised by planting disease-free seed potatoes.[28] Even so, seed quality has been identified as a major limiting factor to successful potato production in a number of countries across sub-Saharan Africa[1,10,29,51] where lack of specialised growers, informal seed systems and the use of unmarketable ware potatoes often result in poor-quality tubers, which produce low yields and tubers with low market values[1,29].

Effective, usually government-regulated, seed potato certification programmes, together with virus testing regimes, have long been implemented in developed countries for the control of seed potato quality.[26-28] Certification thresholds or disease tolerances are set to limit secondary virus transmission from infected seed tubers to daughter tubers and to limit primary infection within a crop in the next season. However, the recent emergence of new strains, e.g. PVY^{NTN} and $\text{PVY}^{\text{N:O}}$, together with potato cultivars that are tolerant, i.e. do not exhibit symptoms, pose new challenges to seed certification programmes.[52] Furthermore, higher temperatures due to climate change may reduce levels of PVY and PLRV[46] below the detection limit of enzyme-linked immunosorbent assays (ELISAs) used for detection in certification schemes. This is especially problematic for seed potatoes produced in low-lying seed potato regions in sub-Saharan Africa where temperature increases are expected to be more severe than in high-lying production areas. New technologies for reliable and sensitive virus detection methods, such as real-time reverse transcriptase polymerase chain reaction (qPCR) assays, should be implemented in schemes for seed certification to overcome the problem.

Some countries in sub-Saharan Africa, e.g. Kenya and South Africa, have introduced seed certification schemes.[25,53] Both largely use ELISA for detection of PVY and PLRV. Due to underdetection, ELISA has been replaced with more sensitive molecular techniques in many European countries.[28] The lack of capacity, aggravated by the cost of certification schemes, and a low demand because farmers are unwilling to pay the high price for quality seed[1,29,54], has delayed the implementation of seed certification schemes in many countries in sub-Saharan Africa. In a survey in eastern Africa (Kenya, Uganda and Ethiopia), only 2% of seed potatoes were sourced from seed growers, whereas 65% originated from own fields and 31% from rural markets.[55] This lack of certified seed could be overcome through government agencies that support smallholder farmers and provide advice through extension services and testing through national agencies. Furthermore, alternative strategies are being developed.[1,29] These include the use of true seed of hybrid potato varieties, which is virus free and easier to transport, benefiting smallholder farmers in remote areas[56], or prolonged seed health in informal systems in sub-Saharan Africa through an 'integrated seed health strategy' where disease resistance is combined with on-farm management[29].

Disease-resistant potato varieties

Resistant varieties, in which the host limits pathogen multiplication, are thought to provide the most efficient way to manage viruses, but the majority of varieties grown currently in sub-Saharan Africa do not possess adequate resistance to PVY or PLRV.[28,57] Furthermore, mature plant resistance has often been overcome by recombinant strains.[58] Breeders have introduced genes for hypersensitive resistance and extreme resistance to PVY.[20,57] Hypersensitive resistance is mostly PVY-strain specific and the death of virus-infected cells leads to localised necrotic lesions. However, as hypersensitive resistance is temperature sensitive, the higher temperatures induced by climate change can be expected to neutralise its beneficial effect.[24] Extreme resistance is effective against a broad range of PVY strains and does not cause visible lesions.[20] Although various molecular techniques (e.g. RNA-mediated resistance, RNA interference and more recently CRISPR/Cas technologies) are available for introducing resistance to viruses, only a few transgenic resistant potato varieties are available and none in developing countries.[36,59] In many countries in sub-Saharan Africa, the introduction of transgenic crops remains a highly contested issue.

Breeding of potato varieties with glandular trichomes, that may reduce aphid settling and thus virus transmission, may be more successful for PLRV than PVY because of the difference in their mode of transmission (persistent versus non-persistent).[57] However, it has been met with limited success because of negative effects on the growth period, tuber size and yield.[57] For recent reviews on PVY-resistant varieties see Valkonen et al.[60] and Kreuze et al.[20], and for PLRV see Halterman et al.[26].

Apart from planting virus-resistant varieties and increasing yield and nutrient content in varieties to maximise the use of the limited area available, more diversified disease-resistant varieties are needed that are at the same time more resource efficient, requiring less water, fertiliser and pesticides to provide greater resilience to extreme weather events.[50,61-63] Some sub-Saharan African countries have initiated breeding programmes, frequently involving the National Agricultural Research System supported by the International Potato Center, to provide varieties suited for local growing conditions.[3,64]

Preventative cultural control

Spatial and temporal isolation

Tubers that exceed virus infection levels set by certification schemes or infected retained tubers in informal seed systems are unsuitable as seed potatoes but are frequently planted as commercial crops, which subsequently serve as virus reservoirs.[47] Geographical isolation and temporal separation of seed from commercial potato plantings and other crops that are potential inoculum sources of PVY or PLRV have been listed amongst the most effective preventative management strategies[28,31,47], which could also be applied by smallholder farmers in sub-Saharan Africa, although effective isolation distances are region specific[31].

Roguing

Another strategy to reduce PVY and PLRV spread within a growing season is roguing – that is the visual inspection and removal of plants expressing symptoms within seed-potato crops (Figure 2d), especially when virus incidence is low.[20,31] For roguing to be effective, seed potato fields require multiple inspections throughout the growing season and it is therefore labour intensive.[31] Infected plants should be removed before aphid numbers increase.[31] In order to recognise infected plants, cultivars expressing symptoms should be grown[47], but this is in conflict with planting disease-resistant varieties that mask symptom expression. In this case, the only alternative to roguing for the elimination of infected plants is detection by laboratory testing, which therefore requires careful consideration.

Elimination of virus sources – volunteer potatoes and weed control

Volunteer potatoes, other susceptible crops and weed species that are hosts of PVY or PLRV are important virus reservoirs.[28] Volunteer potatoes, which are plants that grow from tubers remaining in the soil after harvest, pose a significant threat as a source of virus inoculum and consequently viruliferous aphids in the next growing season, especially if warmer winters enhance their survival, and should be removed before the emergence of new plantings.[28] Another aspect to reduce virus inoculum is weed management as the host ranges of PVY and PLRV span over several families.[65,66]

Crop mulching, intercropping, crop borders

Various options are available to reduce aphid landing in potato fields. The rationale is to create less contrast between the green plant canopy and the soil in order to lower aphid landing rates in seed potato fields.[28] Straw mulches and intercropping with cereals, for example, may reduce PVY spread but may be expensive strategies that are effective only before the canopy closes and may require removal.[28,47] Crop borders consisting of non-virus host plants rely on the same principle. Aphids tend to land in high numbers at field edges due to the contrast in light reflected from the soil and the plants.[49] Aphid landing in the main crop is reduced by displacing the edge of the main field with a non-virus host plant. Crop borders for the management of non-persistent viruses have been reviewed by Schröder et al.[49] Crop borders may be suitable for smallholder farmers in sub-Saharan Africa, whose fields tend to be smaller than those of commercial farmers, as the area needed for a border depends on field size. Crop borders consisting of non-virus crops that are already part of a farming system, e.g. maize or cereals, may provide additional support for smallholder farmers.

Aphid monitoring

Aphid vector species composition and abundance vary greatly with time of year and region.[30,67] Thus, aphid monitoring is a key aspect of managing virus spread. Regular aphid monitoring data enable growers strategically to target location and timing of control measures, to optimise the timing of planting, haulm destruction and harvest. Aphid vector species composition together with their virus transmission efficiency and abundance are used to calculate vector pressure indices for specific regions.[30]

Aphid flight activity is usually monitored with suction traps, often in combination with yellow water traps to provide rapid information on vector pressure (Figure 3). The height of suction traps and the variation in topography determine the area over which aphids are sampled. Suction traps commonly used are 1.8, 8 or 12.2 m high.[68] Traps above 10 m height provide random aerial samples of aphids. Suction traps with a height of 1.8 and 8 m usually monitor aphids at local level. However, depending on the landscape, trap catches of 8-m traps may be representative of aphid flight activity over a 30-km radius.[69] South Africa has an extensive suction-trap network and seed potato farmers receive weekly information on aphid numbers and vector pressure to alert growers to the risk of PVY and PLRV spread.[30] Establishment and maintenance of aphid monitoring programmes may be challenging, because of the cost involved and the difficulty in identifying aphid species, especially for smallholder farmers. However, government- or industry-supported aphid monitoring initiatives should be considered and are recommended as they can be hugely beneficial for controlling viral spread.

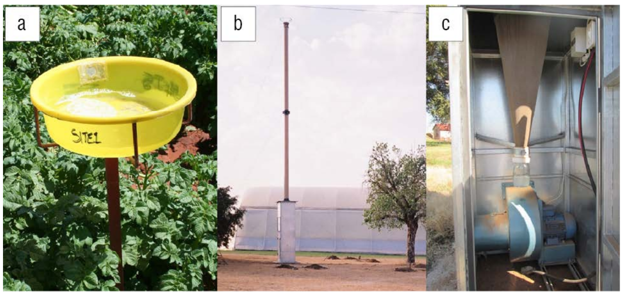


Figure 3: Traps used for aphid monitoring: (a) yellow bucket trap; (b) 12.2-m Rothamsted-type suction trap; and (c) inside of a suction trap showing the insect collection jar.

Planting and harvesting dates

The risk of virus transmission by an increase in aphid vector numbers can be reduced through adjustment of planting and harvesting dates to avoid peak vector activity[47,70], which is region specific[30,39,67]. However, this strategy is dependent on aphid monitoring systems being in place.

Chemical control

The longer transmission time of PLRV compared to PVY makes it easier to manage virus spread with chemical control because insecticides may affect aphid vectors before they can transmit the virus.[44] Synthetic insecticides may not be effective in preventing PVY transmission but may be effective in reducing aphid populations[49] and are one of the main methods for the management of PVY and PLRV. Chemical control using insecticides and mineral oils has been reviewed by Dupuis et al.[28], Lacomme et al.[30] and Yang et al.[71] Mineral oil may reduce PVY spread but its effectiveness depends on environmental conditions.[28,71] In African countries, farmers have been reluctant to use mineral oils because of concerns of phytotoxicity at high temperatures and potential yield loss.[72] Synthetic insecticides for smallholder farmers in sub-Saharan Africa are often not available or affordable.[59]

Predictive models

The complex interactions of different abiotic (e.g. climate change) and biotic stressors (e.g. plant pathogens and insect vectors) on plant growth make it challenging to predict the risk of plant disease development and spread. Climate modelling has progressed over the past years with models being able to guide farmers in planning climate change adaptation strategies.[73] However, adoption of forecasting models for decision-making in sub-Saharan Africa by smallholder and commercial farmers alike has been limited due to lack of sufficient forecasting skills and perceived lack of relevance of forecasting models for specific farming decisions.[74]

New technologies

A variety of new and emerging technologies are being developed to improve virus disease management (e.g. through detection of diseased plants, insect infestations) or to alleviate climate change impact on virus outbreaks at various geographical levels.[36] To improve virus detection, management and prediction, new detection technologies should be implemented, e.g. qPCR. Innovations to provide decision support and curb virus spread include remote sensing, machine learning, aerial surveillance, and precision agriculture.[36,75-77] For example, Gómez et al.[78] developed a model to predict potato yield using satellite remote sensing and machine learning. Griffel et al.[79] proposed the use of support vector machine classification, based on machine learning and using different spectral profiles of PVY-infected and uninfected plants, for the detection of PVY infestations. Furthermore, technologies have been developed to identify areas of insect infestation, including aphids, based on plant stress.[80]

Conclusion

Current knowledge on the effect of climate change on plant disease management is limited. However, various measures may alleviate the predicted impact of climate change on the spread of PVY and PLRV and their aphid vectors. Future work in sub-Saharan Africa should concentrate on improving seed quality, currently a major constraint, especially for smallholder farmers, together with the development of region-specific management programmes that include cultural control methods. Another aspect is breeding for more disease-resistant varieties that (1) are more diversified to have a greater pool of varieties to choose from for different growth conditions, (2) provide greater resilience to extreme weather events, (3) have a higher nutrient content and yield to maximise the use of the area available, and (4) are more resource efficient. Further research should be directed at innovative technologies to improve disease detection, management and prediction. Considerable progress has been made in predictive modelling and its application in crop production, and research should be directed at improving the adoption and implementation thereof in sub-Saharan Africa. However, key to the implementation of any of these advances will be communication so that the benefits of these new technologies can be understood by stakeholders.

Competing interests

We declare that there are no competing interests.

Authors' contributions

K.K. and J.E.v.d.W. jointly conceived and wrote the article.

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