REVIEW

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Seed degeneration in potato: the need for an integrated seed health strategy to mitigate the problem in developing countries

S. Thomas-Sharma[a]*, A. Abdurahman[b], S. Ali[c], J. L. Andrade-Piedra[d], S. Bao[e], A. O. Charkowski[f], D. Crook[g], M. Kadian[c], P. Kromann[h], P. C. Struik[b], L. Torrance[i], K. A. Garrett[aj] and G. A. Forbes[g]

[a]Department of Plant Pathology, Kansas State University, Manhattan, KS, USA; [b]Centre for Crop Systems Analysis, Plant Sciences, Wageningen University, Wageningen, The Netherlands; [c]International Potato Center, New Delhi, India; [d]International Potato Center, Lima, Peru; [e]Potato E&T Research Center, Inner Mongolia University, Hohhot, China; [f]Department of Plant Pathology, University of Wisconsin-Madison, Madison, WI, USA; [g]International Potato Center, Kunming, China; [h]International Potato Center, Quito, Ecuador; [i]Cell and Molecular Sciences, The James Hutton Institute, Dundee, UK; and [j]Institute for Sustainable Food Systems and Plant Pathology Department, University of Florida, Gainesville, FL, USA

Seed potato degeneration, the reduction in yield or quality caused by an accumulation of pathogens and pests in planting material due to successive cycles of vegetative propagation, has been a long-standing production challenge for potato growers around the world. In developed countries this problem has been overcome by general access to and frequent use of seed, produced by specialized growers, that has been certified to have pathogen and pest incidence below established thresholds, often referred to as certified seed. The success of certified seed in developed countries has concentrated the research and development agenda on the establishment of similar systems in developing countries. Despite these efforts, certified seed has had little penetration into the informal seed systems currently in place in most developing countries. Small-scale farmers in these countries continue to plant seed tubers acquired through the informal seed system, i.e. produced on-farm or acquired from neighbours or local markets. Informal seed tubers frequently have poor health status, leading to significant reductions in yield and/or market value. This review emphasizes the need to refocus management efforts in developing countries on improving the health status of seed tubers in the informal system by integrating disease resistance and on-farm management tools with strategic seed replacement. This 'integrated seed health strategy' can also prolong the good health status of plants derived from certified seed, which would otherwise be diminished due to potential rapid infection from neighbouring fields. Knowledge gaps, development challenges and impacts of this integrated seed health strategy are discussed.

Keywords: certified seed, potato virus, quality-declared seed, seed degeneration, seed potato, *Solanum tuberosum*

Introduction

Pathogen and pest build-up in potato seed tubers (seed degeneration) is arguably one of the primary causes of low potato productivity in developing countries (Fuglie, 2007; Gildemacher *et al*., 2009; Cromme *et al*., 2010). The commonly proposed solution to this problem has been to increase availability and farmers' access to seed material produced off-farm by specialized seed producers, often government-regulated to certify a minimum health status (Cromme *et al*., 2010; Frost *et al*., 2013; Mateus-Rodriguez *et al*., 2013; Kaguongo *et al*., 2014). However, certified seed has had little penetration into local seed systems in developing countries (Tripp, 1997; Thiele, 1999). Because most farmers continue to use farm-/neighbour-saved seed or seed from informal seed producers, improving the health of on-farm seed material is necessary. This review discusses how advocating the use of certified seed as a silver bullet to manage degeneration may be overly simplistic, and how integrating host resistance and on-farm management tools with strategic seed replacement with certified seed (or other similar sources of high quality seed such as 'quality-declared seed') will make degeneration management in developing countries more resilient. Although the principles of integrated disease management are established for many diseases, the authors are not aware of papers discussing its importance for the management of vegetative seed material. A move towards an 'integrated seed health strategy' would require amendments to existing research and development agendas, but such a paradigm shift should improve the productivity of vegetatively propagated crops in general, including food security staples such as potato, and therefore the livelihood of smallholder farmers.

*E-mail: thomasuga@gmail.com

Potato (*Solanum tuberosum*) is the third most important food crop globally (FAO, 2013), and over half of all production occurs in developing countries (Devaux *et al*., 2014). The high yield potential of potato per hectare of arable land, good nutritive value, and cooking versatility have led to a tripling of potato consumption in the developing world, from 6 kg/capita year^{-1} in 1969 to 18 kg/capita year^{-1} in 2009 (Lutaladio & Castaldi, 2009). Potato's short cropping cycle allows it to serve as a hunger-breaking crop, and makes it suitable for intercropping and double cropping, especially in cereal-based production systems in Africa and Asia (Cromme *et al*., 2010) and in cropping systems where the main crop has a long establishment period, such as sugarcane plantations in Mauritius (Govinden, 1990). However, potato yields are relatively low in developing countries (Table 1; FAO, 2013) and seed degeneration is considered a major cause of this low productivity (Fuglie, 2007; Gildemacher *et al*., 2009; Cromme *et al*., 2010).

Potatoes are primarily propagated vegetatively via tubers, although sexual propagation via botanical seed, called true potato seed (TPS), is also possible. In general, pathogens pass more readily to asexual propagules than to sexual propagules, and so, in potato, seed tubers are much more likely to harbour a wide range of pathogens compared with TPS. Potatoes grow below ground and are exposed to many soilborne pathogens and pests, presenting additional challenges to maintain the phytosanitary quality of seed tubers. Potato tubers used as planting material are generally referred to as 'seed tubers' or simply 'seed'. Here, the use of the term 'seed' refers to seed tubers, unless otherwise specified, and 'seedborne' refers to those pathogens and pests present in vegetative tubers used as planting material.

Table 1 Per capita consumption and yield of potato in selected countries (FAO, 2011, 2013)

Country	Per capita consumption, 2011 (kg year^{-1})	Yield, 2013 (tonnes ha^{-1})
Developing countries		
Angola	27.7	6.3
Bangladesh	45.2	19.4
Bolivia	66.0	5.8
China	41.2	15.4
Colombia	27.4	18.6
Ecuador	18.9	7.3
Fiji	26.9	6.1
India	25.0	22.8
Kazakhstan	108.2	18.2
Kyrgyzstan	100.8	16.6
Libya	34.7	19.7
Malawi	106.8	17.5
Nepal	75.1	13.6
Peru	82.4	14.4
Rwanda	99.9	13.6
Tunisia	30.3	14.6
Industrialized countries		
Belgium	105.9	46.2
Denmark	59.7	40.0
France	54.5	43.4
United Kingdom	100.8	40.1
USA	55.6	46.6

To facilitate this review, general definitions for informal and formal seed systems from Almekinders (2000) are employed. The informal seed sector is usually defined as all activities related to seed production, management and use, involving mostly small-scale farmers. In contrast, the formal sector includes activities related to seed production, management and use overseen by the public and commercial sector. Informal seed may be produced on-farm or acquired locally (e.g. markets, neighbours); formal seed is purchased from specialized growers and seed quality is generally formally regulated by public institutions through a seed certification programme. As Almekinders (2000) notes, a clear distinction between the two systems does not always exist and in many developing countries semi-formal systems with intermediate forms (e.g. systems with quality-declared seed) exist. However, these definitions are useful for advancing a discussion on potato seed degeneration.

This review discusses the complex nature of potato seed degeneration, addressing epidemiological, socioeconomic, management and governance perspectives. More specifically, this paper aims to (i) synthesize the literature on the nature, causes and importance of potato seed degeneration; (ii) describe perceptions of why and how the 'certified seed replacement paradigm' has shaped the research and development agenda in developing countries; (iii) present an evidence-based integrated approach to prevent or slow down degeneration of potato seed material that is more appropriate for developing countries; and (iv) identify knowledge gaps and research challenges for formulating a potato seed health strategy.

Nature, causes and importance of potato seed degeneration

Definitions of seed degeneration

The focus on potato seed degeneration in the scientific literature was most evident several years after seed certification programmes began (in the early 1900s) in Europe and the USA (Shepard & Claftin, 1975; Frost et al., 2013).The fact that degeneration was primarily caused by viruses was discovered then and studies that unraveled the epidemiological principles of degeneration were initiated (Whipple, 1919; Folsom *et* *al*., 1926; Brown, 1929; Whitehead, 1930). Accordingly, Whitehead (1930) defined degeneration as an increase in the incidence of plants with virus symptoms and a concomitant reduction in yield. It is now known that increased incidence and/or severity of non-viral seedborne pathogens can also contribute to yield reductions. Moreover, damage caused by pathogens and pests reduces not only yield, but also market value. Struik & Wiersema (1999) defined degeneration as 'a decrease in the quality of the seed [tubers] from continued propagation, mostly caused by a decrease in health status'. Building on these definitions and specifying the causes of degeneration, seed degeneration can be defined as 'an increase in pest and/or pathogen incidence or severity, associated with reduction in yield or quality of seed tubers over successive cycles of vegetative propagation'.

Previous work on the quality of vegetative seed has been less structured than that of sexual seed, for which research methods, concepts and definitions have been defined by the International Seed Testing Association (ISTA, 2014). However, some ISTA definitions are also broadly applicable to vegetative seed, such as the term 'seed quality' (Table 2; Fig. 1).

Some authors include disorders resulting from advanced physiological age of tubers as part of seed degeneration (Kawakami, 1962; Iritani, 1968). However, the authors of this review consider physiological age, physiological disorders and physical abnormalities, which are generally reversible within one generation of adequate management, to be components of potato seed quality. This is differentiated from pest- or pathogen-induced seed degeneration, which tends to increase over time in the absence of management. Unlike physiological disorders, pathogens can also spread to neighbouring plants. The authors propose the term 'seed health' to refer specifically to the severity and/or incidence of pests and pathogens in tubers; and seed health would then be another characteristic of seed quality (Fig. 1). This article thus describes degeneration

Table 2 Glossary of key terms related to potato seed degeneration and its management

Certified seed	Seed produced within the formal seed system by specialized growers that has been certified to have pathogen and/or pest incidence or severity below established thresholds. Commonly used synonyms include 'clean seed' and 'disease-free seed'
Efficiency of autoinfection	Percentage of infected progeny tubers obtained from an infected mother plant (Bertschinger, 1992)
Formal seed system	The activities of the public and commercial sector, including seed growers, related to seed production, management and use; seed quality is generally formally regulated by public institutions (Almekinders, 2000)
Informal seed system	The activities of mostly small-scale farmers, relating to seed production, management and use (Almekinders, 2000)
Physiological age	Physiological status of the seed tuber as affected by its chronological age and other modifying factors such as growth history, storage conditions and treatments that influence tuber dormancy, sprouting and growth vigour (Struik & Wiersema, 1999)
Plant selection	Selection of symptomless plants as seed source under high disease intensity (positive selection) or rejection of plants with symptoms as seed source under low disease intensity (negative selection)
Potato value chains	All activities and networks of functional relationships necessary for achieving production and use of potato (Cromme *et al*., 2010)
Quality-declared seed	Improved seed where some flexibility is allowed in implementing quality standards; used as an alternative in regions where activities to maintain high standards are difficult (FAO, 2006)
Roguing	Removal of plants with symptoms within the growing season
Seed degeneration	An increase in pest and/or pathogen incidence or severity, associated with reduction in yield or quality of seed over successive cycles of vegetative propagation. Incidence of degeneration refers to the frequency of tubers infected with degenerative pathogens or pests in a seed lot. Severity of degeneration refers to pathogen and/or pest load (example virus titre) per individual diseased tuber
Seed health	An attribute of seed quality that refers specifically to the severity and/or incidence of pathogens and pests
Seed quality	All attributes of the seed tuber that affect its value, including genetic purity, physical condition (size, shape, wounds), health condition (pathogen and/or pests) and physiological age
Seed systems	All institutional and non-institutional components involved in the production, management, replacement and distribution of seed tubers (Thiele, 1999)
Technography	A methodological approach in social science that uses ethnographic descriptions of technology to examine human x machine/tool interaction (Jansen & Vellema, 2011)
Tuber-uniting	Practice of dividing seed tubers into four pieces and planting them consecutively; it increases the efficacy of roguing because groups of infected plants are more easily identified than individual plants and allows the removal of all of the seed pieces that originated from an infected tuber

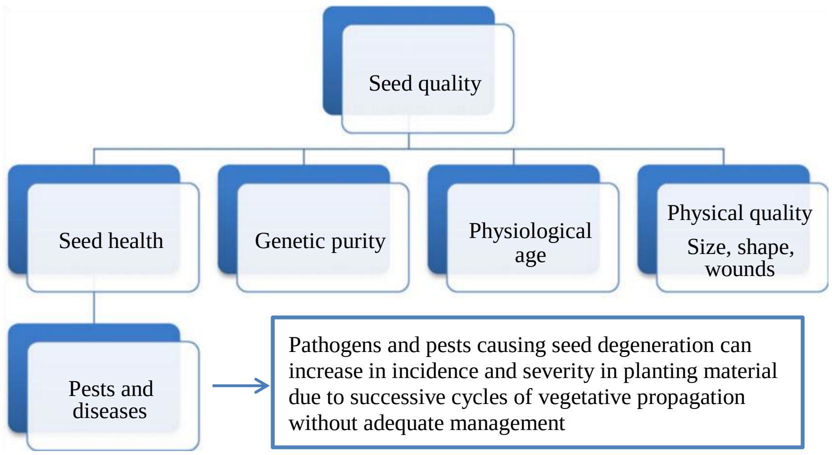

Figure 1 Proposed seed quality terminology for potato vegetative propagation. Seed quality refers to all attributes of seed tubers including genetic purity, physical condition (size, shape, wounds), health condition (pathogens and/or pests) and physiological age (including factors beyond tuber's chronological age, such as growth history, storage conditions and treatments that influence tuber dormancy, sprouting and growth vigour). Seed health refers specifically to the severity and/or incidence of pests/pathogens in seed and includes the effects of seed degeneration.

of potato seed as a manifestation of decreasing seed health, i.e. an increase in the incidence of pathogens/pests in seed.

It should also be noted that there are sometimes limits to the degree of degeneration in following generations of seed. For example, when degenerated seed is planted, host resistance to disease may protect the host population from further seed degeneration under normal production conditions. There may also be factors that lead to regeneration of seed from these plantings, such as weather unfavourable to pathogen growth.

Causes of seed degeneration in potato

Seed degeneration in potato has a complex aetiology. In addition to the many soilborne pathogens persisting in close proximity with maturing tubers, many air- or vector-borne pathogens also readily become seedborne, along with some insects and nematodes (Struik & Wiersema, 1999). Up to 40 different pathogens cause soilborne diseases of potato (Fiers *et al*., 2012); however, not all are significant, nor do all survive well enough in tubers to be considered important as seedborne pathogens (Fig. 2). Furthermore, although all degeneration causing pathogens are seedborne by definition, not all seedborne pathogens contribute significantly to degeneration because they do not readily increase in incidence or severity in the seed over subsequent generations [e.g. the potato black dot pathogen *Colletotrichum coccodes* (Dung *et al*., 2012)]. Thus, although many potato pathogens may be considered seedborne, potato viruses, which generally spread systemically from parent to progeny tubers, have long been recognized as the primary cause of degeneration (Salazar, 1996; Solomon-Blackburn & Barker, 2001). Of the *c*. 30 viruses infecting potatoes, *Potato virus Y* (PVY), *Potato leafroll virus* (PLRV) and *Potato virus X* (PVX) are the most important in production systems worldwide (Scholthof *et al*., 2011), with PVX considered more important in combination with PVY than by itself (Salazar, 1996; Draper *et al*., 2002).

The relative importance of degenerative pathogens and pests varies between geographic regions, and soilborne pathogens and pests that readily become seedborne can contribute significantly towards regeneration (Fig. 2). For example, in a study in the high-altitude production areas of the Ecuadorian Andes, significant yield reduction was attributed to *Rhizoctonia solani*, found at an incidence of up to 78% in farmers' seed, while the generally important viruses PLRV and PVY were at an incidence of <3% (Fankhauser, 2000). At lower altitudes in many tropical and subtropical countries, *Ralstonia solanacearum*, the cause of bacterial wilt, is an important component of degeneration with an incidence of up to 36% in tubers from some farms in Kenya (Mwangi *et al*., 2008). *Dickeya* spp., causing blackleg and soft rot, can spread readily as latent systemic infections in seed, and these species are emerging as major pathogens in many parts of Europe and in Israel (Toth *et al*., 2011). *Pectobacterium* spp. causing blackleg and soft rot, *Clavibacter michiganensis* subsp. *sepedonicus* causing soft rot and ring rot, and powdery scab caused by *Spongospora subterranea* are other pathogens that may contribute significantly to seed degeneration (Struik & Wiersema, 1999). Nematodes such as *Globodera* spp. and *Meloidogyne* spp., whose eggs, cysts and larvae become seedborne, are important pests of seed, causing seed degeneration (Struik & Wiersema, 1999). Seedborne insect pests, such as potato tuber moth, can also be considered important causes of degeneration in tropical countries, as they may readily become seedborne and have multiple generations in the field and in storage (Sileshi & Teriessa, 2001; Golizadeh *et al*., 2014). Similarly, newly discovered viruses (Li *et al*., 2013), as well as emerging epidemics of *Potato yellow vein virus* in many South American countries (Salazar *et al*., 2000), potato purple top phytoplasma in the Pacific

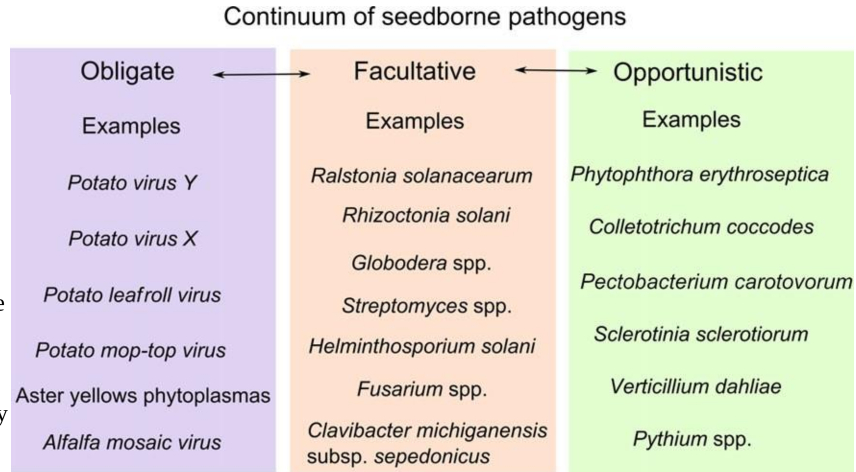

Figure 2 Classification of seedborne potato pathogens based on the necessity of tubers for pathogen survival between host generations. Seedborne pathogens fall in a continuum from being obligate seedborne pathogens (cause systemic infections, with tubers playing a predominant role in survival), facultative seedborne pathogens (tuber infections are common but so is survival in the abiotic environment), and opportunistic seedborne pathogens (found occasionally on tubers largely as a consequence of their soilborne nature).

Northwest of the United States (Crosslin *et al*., 2011) and zebra chip disease (‘*Candidatus* Liberibacter solanacearum’) in many countries (Henne *et al*., 2010) may develop into significant seed degeneration threats.

Factors affecting the rate of seed degeneration

The rate and expression of seed degeneration are directly and indirectly influenced by numerous environmental parameters and geographical characteristics that act not only on the host and pathogen and their interaction, but also modify vector dynamics. Whitehead (1930) observed that two experimental stations, *c*. 50 km apart in North Wales, had different patterns of potato degeneration. In the Andes, degeneration is much slower at altitudes of >2800 m above sea level (m a.s.l.) and even further reduced at altitudes above 3500 m a.s.l. (Thiele, 1999). Studies in the Andes have shown that potato viruses are sometimes found at very low incidences in potato land races or varieties that have been exposed to natural conditions for untold generations (Bertschinger *et al*., 1990; Fankhauser, 2000). Low levels of seed degeneration at high elevations could be because of reduced multiplication of vector and/or pathogen, which could limit disease spread. Altitude (and correlated temperature) may also affect host physiology and subsequently reduce transmission of pathogens from mother tubers to daughter tubers (Bertschinger *et al*., 1995a).

Research in Peru also indicates potentially complex host–pathogen interactions in degenerative diseases. One study found that virus incidence could decrease in subsequent generations (i.e. not pass from an infected mother plant to all progeny tubers) and that this phenomenon was strongly favoured by higher altitudes (Bertschinger, 1992). Bertschinger (1992) used the term ‘reduced efficiency of autoinfection’ (see Table 2 for definition) to describe this phenomenon. This may be one manifestation of host plant resistance to viruses, while other forms of resistance involving both the virus and vector also exist (Radcliffe & Ragsdale, 2002; Palukaitis & Carr, 2008).

Variability in the extent of adoption and efficacy of management practices generates differences in local inoculum and pest pressure, in turn influencing both farm-level and regional epidemics. The efficacy of management practices such as selection of symptom-free planting material and roguing depends heavily on detection of disease. Symptom-based detection can be rapidly and inexpensively applied over large areas, but may miss plants with masked symptoms and latent infections (Robert *et al*., 2000). Serological- and nucleic acid-based techniques have increased the sensitivity, specificity and speed of identifying diseased samples. However, it should be noted that high accuracy disease management might select for viruses with mild visual symptoms, making symptom recognition-based control strategies such as roguing and plant selection (see Table 2 for definitions) less effective (van den Bosch *et al*., 2007; Döring, 2011). Because access to modern diagnostic kits is limited in developing countries, field detection of disease continues to rely on farmers’ or inspectors’ experience in recognizing symptoms.

Consequences of degeneration for ware potato production in developing countries

As with many constraints to crop productivity, accurate quantitative data on the socioeconomic consequences of potato seed degeneration are unavailable for most developing countries. Numerous studies of degeneration have been conducted by comparing plantings of healthy seed with plantings of seed exposed to natural infection for a known number of generations, but it is challenging to extrapolate these results to a larger geographic scale. These trials give an indication of the potential for losses but are not necessarily good indicators of yield losses in farmers' fields. For example, experimental studies rarely account for yield compensation, where healthy plants use the extra space from reduced haulm growth of their diseased neighbours to increase productivity (Struik & Wiersema, 1999). In addition, there are inherent difficulties in determining the impact of a complex problem like degeneration, and it appears that there has been little effort at assessment because the problem is of minor importance in industrialized countries, owing to the 'certified seed replacement paradigm' (discussed below). Nonetheless, a brief review is provided of some of the literature available on yield losses in specific cases of potato seed degeneration.

In experimental plots where infected seed tubers were used, estimated losses due to PVY ranged from 29 to 85% (Hossain *et al*., 1994; Mannan *et al*., 2008; Rahman *et al*., 2010), and for PLRV from 29 to 78% (Whitehead, 1924; Rahman & Akanda, 2010). Yield loss due to bacterial wilt varies with cultivar, climate, soil type and prevailing pathogen strains, and was reported to range from 30 to 90% in Bolivia (Elphinstone, 2005) and from 30 to 75% in parts of East Africa with occasional losses of 100% (Lemaga *et al*., 2005). These studies were conducted over varying numbers of years, in diverse potato-growing locations of the world and have used naturally infected plant populations or intentional mixtures of healthy and diseased plants to quantify the relationship between incidence and loss. In an example of the latter type of study, Nolte *et al*. (2004) concluded that a 1% increase in incidence of seedborne PVY resulted in a tuber yield reduction of 0.17–0.18 t ha^{-1}, their model explaining 67–82% of variation in yield. Averaging over yearly and varietal yield differences, this translated into a maximum yield reduction of 30–40% in a crop with 100% incidence of seedborne PVY.

Another approach to estimating yield loss due to degeneration comes from studies involving multiple on farm trials where interventions have been aimed at curbing degeneration. Researchers in sub-Saharan Africa have observed yield increases of *c*. 30% on average with one season of positive selection (Gildemacher *et al*., 2011; Schulte-Geldermann *et al*., 2012). Given that positive selection is not 100% efficient, as farmers miss latently or even mildly infected plants, some yield loss would occur despite positive selection. Thus, these studies present a highly conservative estimate of actual yield losses in farmers' fields. A recent study in Ecuador in farmers' fields indicated that up to 29% of the yield variability could be explained by seed health (Panchi *et al*., 2012). Many potato workers in developing countries would probably consider 30% to be an underestimate of potential yield increase due to degeneration management, and additional efforts to accurately measure losses due to degeneration in farmers' fields, and not simply losses to disease within a season, are warranted.

Approaches to degeneration management

The certified seed replacement paradigm

From the literature of the early part of the twentieth century, it is evident that degeneration of potato was a major concern among producers and researchers (Massee, 1907; Brown, 1929; Whitehead, 1930). This concern, and the empirical observations of farmers that use of healthy seed could improve yield, quickly led to the implementation of certified seed production systems aimed at making healthy seed of improved varieties readily available to farmers in Western Europe and North America (Shepard & Claftin, 1975; Frost *et al*., 2013). This certified seed was produced and distributed through strictly regulated formal seed systems involving federal or state governments, land grant universities and grower associations (Shepard & Claftin, 1975). The systems evolved over the decades to produce seed of continuously higher quality, and were estimated to increase yields by 70–100% when high-quality seed was used regularly (Shepard & Claftin, 1975; Monares, 1988).

The formal potato seed systems developed particularly quickly in industrialized economies where potato was the main staple food and hugely important to national food security (Shepard & Claftin, 1975). Economic forces together with institutional and social factors were favourable to systems of commodity development based on protection of property rights and profit mechanisms (Vanloqueren & Baret, 2009). Phytosanitary certification also became a necessity to facilitate international trade of seed potato while simultaneously limiting the movement of various quarantine pests and pathogens (deGraaf, 1994). Thus, owing to effective certified seed systems in industrialized countries, regular or even yearly replacement of seed with certified seed became the norm. The certified seed replacement paradigm became institutionalized (Fig. 3) and the problem of potato seed degeneration was relegated to a minor echelon in the hierarchy of farmer and researcher concerns.

Failure of the certified seed replacement paradigm in developing countries

The situation has been very different in the developing world where socioeconomic and agroecological contexts are different from the economies, governance and temperate climate in most of the industrialized countries. Given the success of formal, certified seed systems in the industrialized countries, the general approach to degeneration management in developing countries has been to establish similar formal seed systems (Monares, 1988; Thiele, 1999; Kadian *et al*., 2009; Labarta, 2013; Pathania *et al*., 2013; Kaguongo *et al*., 2014). These efforts have to a large extent failed as evidenced by the limited use of formal seed in the majority of developing countries (Table 3). In South and West Asia, technology for quality seed production is available, but many countries lack the infrastructure, resources, trained personnel and institutions (whether governmental or private sector) to guarantee proper implementation (Kadian *et al*., 2007). Kenya has an institutional framework for a formal seed system but lacks enforcement and economic backing to ensure quality (Gildemacher *et al*., 2009). Moreover, in Kenya and many other African countries, there are high levels of soilborne nematode, fungal and bacterial diseases, virus vectors, and solanaceous weed hosts that harbour viruses. These factors all contribute to quick contamination of healthy planting material (Were *et al*., 2013). An exception to the limited use of certified seed in Africa can be found in South Africa, where large-scale commercial growers use certified seed produced in a system similar to the ones in place in Europe and North America (Potato Certification Service, 2015).

Undoubtedly, numerous factors contribute to the lack of success of efforts to implement formal seed systems in developing countries, including economic factors, beyond the scope of this synthesis. Thiele (1999) analysed formal seed systems in developing countries in detail, finding many potential reasons for the low demand and supply of certified seed, which include the bulky and perishable nature of seed, production risks due to adverse climate and limited access to resources, the high costs of formally certified seed, limited infrastructure and resources for formal seed programmes to ensure quality, uncertain connections to markets due to fluctuating prices, and other factors that result in poorly connected value chains. In developing countries, farmers obtain most seed from their own ware production fields, or acquire seed locally from family, neighbours, NGOs or rural markets. Specialized informal seed growers frequently provide seed only to local areas. For example, about 29% of potato fields in the North Shewa region of Ethiopia used seed from local specialized producers, while use of this kind of seed was estimated to be <1% in Kenya and <4% in Uganda (Gildemacher *et al*., 2009). Tufa (2013) noted that in Ethiopia the price difference between seed and ware potatoes was so small (close to zero) that specialized seed growers are rarely rewarded for any additional efforts taken to produce high quality seed.

The low demand for expensive certified seed also highlights the sometimes unacceptable, economic cost related to elaborate certification programmes. Although the economics behind any given seed system are multifaceted and difficult to determine in detail, it is apparent that there is a cost related to each disease tolerance threshold applied in a system, and the more stringent the threshold, the higher the cost is likely to be. For example, in the Wisconsin seed potato certification programme in the USA, the cost of seed of virus-susceptible lines is higher because it takes greater effort to keep the tubers below the tolerance threshold for diseases (A. O. Charkowski, personal observation). Consequently, in risk prone and suboptimal production areas, high cost degeneration control practices (i.e. the certified seed replacement paradigm) make less economic sense. In addition, differences in priorities, lack of infrastructure, rampant corruption, absence of enforcement, and limited trust can add to the inherent difficulties in ensuring the success of formal seed systems.

Toward an integrated seed health strategy

Before certified seed systems were implemented in the industrialized countries, farmers and researchers

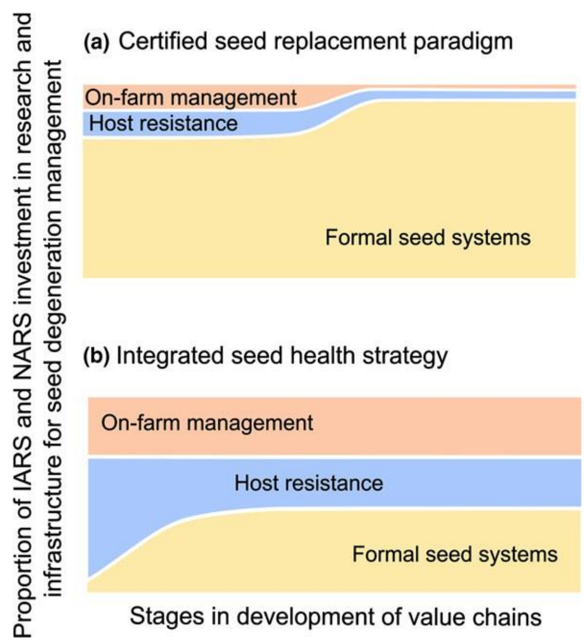

Figure 3 Proportion of investment by international agricultural research systems (IARS) and national agricultural research systems (NARS) in research and infrastructure for seed degeneration management in relation to the stages in development of value chains. As links to potato value chains are strengthened, (a) the certified seed replacement paradigm, which shapes current research and development, focuses on the establishment and improvement of formal seed systems with little investment in host resistance and on-farm management strategies, and (b) the integrated seed health strategy, proposed here as an alternative, focuses on integrating host resistance and on-farm management with strategic use of certified seed from formal seed systems.

Table 3 Percentage contribution of formal potato seed system[a] and informal potato seed systems[b] in some developing countries

Country	Formal seed system	Informal seed system	Reference
Afghanistan	0	100	Kadian *et al*. (2007)
Bangladesh	5	95	Ilangantileke *et al*. (2001)
Bhutan	2	98	Kadian *et al*. (2007)
Bolivia	2	98	Hidalgo *et al*. (2009)
China	20	80	Muthoni *et al*. (2013)
Columbia	2–10	90–98	FEDEPAPA (2010), Guzman-Barney *et al*. (2012)
Ecuador	1–3	97–99	Thiele (1999), ESPAC (2012)
Ethiopia	11[c]	89[c]	Gildemacher *et al*. (2009)
India	20	80	Kadian *et al*. (2007)
Indonesia	6	94	Muthoni *et al*. (2013)
Kenya	0.5[c]	99.5[c]	Gildemacher *et al*. (2009)
Pakistan	5	95	Muthoni *et al*. (2013)
Peru	0.5	99	Hidalgo *et al*. (2009)
Uganda	4[c]	96[c]	Gildemacher *et al*. (2009)

[a]Formal potato seed system includes regulated certified seed and tubers from specialized seed producers.
[b]Informal potato seed systems include seed produced on-farm or acquired from neighbours or local markets.
[c]Estimates from Gildemacher *et al*. (2009) have been averaged across districts and summarized to include 'seed grower' under the formal seed system and 'own field', 'neighbour' and 'rural markets' categories under the informal seed systems.

emphasized resistant varieties (Orton, 1914) as well as a number of on-farm management techniques to maintain or improve seed health, such as establishing seed plots, tuber-uniting, roguing and plant selection (see Table 2 for definitions) (Whipple, 1919). Such techniques continue to be routinely used by seed producers in certified seed production systems (Frost *et al*., 2013). In the Andes, farmers have traditionally sought seed from higher altitudes knowing it was of higher quality (Thiele, 1999). Furthermore, there is reason to believe that many of the native potato varieties have resistance and/or tolerance to the major yield-reducing viruses – indeed, major resistance genes against PVY, PVX and PLRV have been found in cultivated and wild potato species from the Andes such as *Solanum andigena* and *Solanum chacoense* (Solomon-Blackburn & Barker, 2001; Velásquez et al., 2007). DiFonzo et al. (1995) determined that the critical threshold for management of green peach aphid could be relaxed depending on the level of PLRV-resistance in potato varieties.

In the case of bacterial wilt management, the combined use of partially resistant varieties, healthy seed, and improved cultural practices resulted in greater reduction in wilt incidence and increased tuber yield compared with applying the components individually (Lemaga *et al*., 2005). For soilborne diseases that are indigenous to a region, planning management at a community level may also be critical. Although the incidence of bacterial wilt can be alarmingly high in many potato growing areas, pathogen prevalence is highly variable (Hayward, 1991). A better understanding of the interaction between environmental factors and management practices at higher levels of geographical aggregation (rather than only in individual fields or farms) is necessary to use this variability to the producers' advantage. Under such circumstances, community-based farmer capacity building programmes for on-farm seed management are likely to create cost-efficient solutions.

These examples represent two major areas of intervention that can be used to manage seed health: host plant resistance and on-farm management practices. Strategic use of these two approaches, together with purchase of certified (or other types of high quality) seed when economically viable, leads to an integrated strategy for managing seed health (Fig. 3). Integration can provide synergies among the three types of intervention. For example, periodic introduction of certified seed into a system may be much more effective if the variety involved has resistance to one or more degeneration pathogens. On-farm practices such as plant selection and vector management would also decrease degeneration in certified tuber stocks, maintaining the value of high quality seed and making the option to buy certified seed every few years more attractive.

Evidence of usefulness of host resistance and on-farm management

Several seed degeneration studies have compared two or more varieties, sometimes with known levels of resistance, and indicated differences in yield loss. Studies in two locations in India indicated that after four seasons of field cultivation the local variety Kufri Jyoti had lower yield reduction due to viral degeneration than did Kufri Giriraj (Ali *et al*., 2013). In Kenya, after four seasons, the overall yield reduction in genotypes resistant to multiple viruses ranged from 5 to 33% while the yield reduction in the local Ugandan and Kenyan varieties ranged from 56 to 58% (John *et al*., 2013). In Uganda and Kenya, where bacterial wilt is endemic but chemical and cultural control is minimal, resistance to bacterial wilt is considered an important attribute of improved varieties. For example, although the variety Rutuku is high yielding with locally preferred red skin and moderate resistance to late blight, it has been abandoned by Ugandan farmers due to its high susceptibility to bacterial wilt (Kaguongo *et al*., 2008). These studies indicate that host plant resistance has potential to reduce the rate of degeneration.

Plant selection involves the use of symptomless plants, identified by visual inspection before senescence, as the seed source for the next season (Bryan, 1983; Gildemacher *et al*., 2011). In field studies with viral diseases, after one cycle of plant selection, this method led to a yield increase of 23–35% (Schulte-Geldermann *et al*., 2012), 28–53% (Gildemacher *et al*., 2011), 39% (Alvarez, 1988) and 7–44% (J. L. Andrade-Piedra, unpublished results), while simultaneously lowering virus incidence. Epidemiologically, plant selection is similar to using certified seed in that it reduces the level of primary inoculum in the field. However, because the method relies on symptom recognition, effective farmer training is critical for the success of this strategy.

Roguing reduces inoculum sources in the field, reducing pathogen spread. This method also relies on farmer training in symptom recognition and works best when growers synchronize roguing over large areas (Sisterson & Stenger, 2013). In potato, studies on the usefulness of roguing against viral diseases indicate variable success. In one study the method reduced tuber infection by PLRV by about 30–45%, but this depended on the level of vector infestation in the field (Ioannou, 1989). Another study indicated that roguing was more effective against PVY than against PLRV and that early roguing was more effective than late roguing (Broadbent *et al*., 1950). Because aphid alighting can be affected by gaps in the crop canopy, roguing giving rise to gaps ≥0.6 m^2 can result in greater incidence of PVY (Davis *et al*., 2009). If infected plants produce useable yield, roguing can reduce overall crop yield (Sisterson & Stenger, 2013). Adjacent healthy plants may compensate for yield loss if diseased plants are removed (Salazar, 1996), but in practice workers in many developing countries have noted that farmers rarely remove plants that may serve as a source of food (G. A. Forbes, personal observation). Although roguing may reduce yield within one season, roguing used over successive cycles of propagation would reduce seed degeneration and thereby increase yield, especially in the absence of other degeneration management strategies. This is assuming that care is taken to move diseased plants (and tubers, if late roguing is practised) away from the yield and destroy them, preventing spread of disease during their removal. Scientific demonstration of the costs and benefits of roguing is needed to clarify its field usefulness.

Early-season crop hygiene, the practice of removing alternate weed hosts and volunteer plants, can delay the onset of disease. Volunteer potato plants (also called groundkeepers), are potato plants growing from TPS or potatoes left behind after harvest and can serve as sources of primary inoculum (Askew & Struik, 2007). Volunteer plants are of particular concern in cool temperature regions where most solanaceous plants die in the winter months and vectors normally overwinter on hosts that do not harbour virus populations (Robert *et al*., 2000). In warmer climates, removal of both alternate hosts and volunteer plants should also be important in reducing initial inoculum, although the authors are not aware of studies that demonstrate this.

Vectors play the most important role in the secondary spread of viruses within a field and, although vector management is an integral part of producing certified seed, it can be expensive and often beyond the reach of small-scale potato farmers. In addition, routine, indiscriminate use of pesticides has resulted in the emergence of resistant populations of aphids (van Toor *et al*., 2009). Alternatively, growing border crops such as soybean, wheat or resistant potato varieties around the edge of a potato field can limit nonpersistently transmitted viruses that are attracted to the colour contrast (brown soil versus green crop) at the edges (Radcliffe & Ragsdale, 2002; Boiteau *et al*., 2009). Other management strategies, such as straw mulching to affect aphid flight activity (Saucke & Döring, 2004), polymer webs used as protective plant cover (Harrewijn *et al*., 1991), pheromone traps, and insecticidal soap to alter aphid feeding, can also be used and may hold greater promise for resource-poor farmers.

The choice of field sites and selection of planting date can also maintain low disease incidence in seed by disease avoidance. Aphid monitoring studies have revealed that vector incidence and resulting virus pressure are much lower at higher elevations (Vucetic *et al*., 2013; Ali *et al*., 2015) and that there are temporal peaks of vector abundance in the field (Carli & Baltaev, 2008). Pre-sprouting tubers prior to planting can result in earlier emergence and escape from pathogens or vectors that are more abundant later in the growing season (Hospers- Brands *et al*., 2008). Ensuring that seed potato plots are harvested before harvest of adjacent fields, thereby avoiding heavy vector flights from adjacent crops, can also reduce spread of disease. Large-scale vector incidence monitoring studies can provide an objective basis for identifying sites and cultivars (early- versus late-maturing) better suited for seed multiplication in a region.

Other management practices such as tuber-uniting, varietal mixtures and crop rotations can also be useful against degeneration. Tuber-uniting is the practice of dividing seed tubers into four pieces and planting them consecutively. The practice increases the efficacy of roguing because groups of infected plants are more easily identified than individual plants and allows the removal of all of the seed pieces that originated from an infected tuber. Tuber-uniting is useful for farmers who plant cut-seed and practice roguing, although sterilization of cutting knives is critical to prevent the spread of bacterial or viral pathogens in a seed lot. The use of varietal mixtures to control *Phytophthora infestans* can reduce disease incidence, especially when highly resistant varieties are included with susceptible varieties (Phillips *et al*., 2005; Garrett *et al*., 2009). For soilborne degenerative diseases, crop rotation plays a major role in lowering field inoculum pressure. Rapeseed used as green manure, compared with rotation with oats, led to a 70–80% reduction in the incidence of *R. solani* in the following season (Larkin & Griffin, 2007), and disease suppression has also been observed against bacterial wilt (*R. solanacearum*) when the legume *Crotalaria falcate* was used in crop rotations (Kakuhenzire *et al*., 2013). In addition to known biofumigant properties of some green manure crops (e.g. *Brassica* spp.), increasing organic matter in the soil encourages the growth of mycophagous soil mesofauna that aid in disease suppression (Scholte & Lootsma, 1998).

Opportunity costs of the certified seed replacement paradigm

Many reasons have been given for the failure of certified seed replacement systems in developing countries (Thiele, 1999). The authors propose that the research and development initiatives that have driven potato seed interventions in developing countries for the last five decades or more (Crissman, 1989; Crissman *et al*., 1993; Kadian *et al*., 2007; Hidalgo *et al*., 2009; Gildemacher *et al*., 2012) need to be critically scrutinized. The near-exclusive emphasis on certified seed replacement systems (Fig. 3) has adversely affected international, national and regional research agendas. Current efforts to deal with the problem of low quality seed potato in developing countries focus on either improving existing formal systems or establishing new ones. Few resources are available to improve host plant resistance levels, refine and implement plant selection at the field level, and promote pest and disease avoidance, all of which may have immediate impact by improving the quality of on-farm seed.

Adding to these challenges are draconian seed laws enforced in some countries. In Kenya, for example, the tolerance for certain diseases such as bacterial wilt is nil for any grade of seed tubers from basic seed (progeny of certified breeder's seed or certified pre-basic seed) to third generation certified seed (progeny of first or second generation certified seed) (Sikinyi, 2000). Similarly, in Uganda, bacterial wilt incidence is required to be nil during any field inspection (Ssebuliba, 2010). Given that bacterial wilt is endemic in many seed production areas, and that there is a lack of resistant varieties, the feasibility of achieving such thresholds is questionable, not to mention the enormous costs and consequently high price of seed tubers necessary to make the operation profitable. In mature systems such as the Wisconsin seed potato certification programme, thresholds were developed based on what works for farmers in an area rather than 'transplanting' thresholds established elsewhere (A. O. Charkowski, personal observation). Similarly, quality-declared seed, where some flexibility is allowed in implementing quality standards, would serve as a good alternative in regions where activities to maintain high standards are difficult (FAO, 2006). Thus, an approach where 'the perfect is the enemy of the good', where establishment of perfect thresholds for disease is given higher priority than using realistic but 'good' thresholds, can slow or derail even the smallest penetration of certified seed into informal seed systems of developing countries.

Conclusions and considerations

The certified seed replacement paradigm, successfully established in developed countries, has had limited impact in improving the health of on-farm seed in developing countries. Because most small-scale farmers get seed material as a by-product of their own ware potato crops or from local informal sources, a degeneration management strategy should include improvement of the health status of seed from these sources. To facilitate integrated and interdisciplinary approaches, the authors consider all seed health problems that may accumulate in tubers over successive cycles of vegetative propagation as causes of degeneration, including some insect pests and nematodes. The integrated seed health strategy, which in addition to strategic use of certified seed encourages the use of host resistance and on-farm management tools, is intended to offer a realistic solution to managing degeneration in informal seed production systems. Some critical research areas that would aid in the implementation of an integrated approach are elaborated below.

Improved estimation of on-farm yield reduction due to seed degeneration

Estimating the impact of agricultural pests on yield is a critical element for prioritizing research agendas and establishing economic thresholds for use of management components. Although yield reduction due to individual pathosystems has been studied, overall reduction due to seed degeneration in the field is rarely the sum of their parts. Synergistic and antagonistic interactions between pathogens can increase or reduce the severity of seed degeneration. Further, as seed degeneration is due to accumulation of pathogens and/or pests over multiple generations, long-term studies of yield reduction are critical for impact assessment. One such globally collaborative study is currently underway as a part of the CGIAR Research Program on Roots, Tubers and Bananas (RTB). Potato seed degeneration trials, aimed at understanding the efficacy of resistance and management practices on seed degeneration, have been established in diverse agroclimatic regions of Ecuador, China, Kenya and Ethiopia.

Better understanding of cultivar resistance to degenerative diseases

Given the near-absence of certified seed replacement in developing countries, it is assumed that host genotype already plays a major role in the level of degeneration currently experienced in those parts of the world. High levels of resistance in individual plants and a mosaic of such hosts in a region can, in theory, reduce disease spread. However, despite the apparent availability of many such cultivars, their acceptance and deployment in a region can be affected by many factors including farmer and end-user preferences, environmental stability of resistance and the incidence of pathogens causing seed degeneration. A deeper appreciation of these factors is important for integrating host resistance into seed degeneration management. Given the multi-pathogen nature of degeneration in many cases, it is also important to understand the overall epidemiological effect of high levels of resistance to one pathogen versus moderate levels of resistance to multiple pathogens. In addition, phenomena such as autoinfection and mature plant resistance vary with elevation, pathogen type and cultivars (Bertschinger, 1992; Radcliffe & Ragsdale, 2002). Studies to clarify whether these phenomena have a heritable genetic basis would greatly aid the development of resistant varieties. Finally, a major impediment to greater use of host plant resistance is the absence of a common, quantitative system for assessing resistance phenotypes.

Interdisciplinary research evaluating the efficiency and adoption of on-farm integrated seed health strategy

Management practices proven to have epidemiological utility should have high efficacy across agroecological zones. Additionally, assessing the cost–benefit ratios of management components (applied for one year and multiple years) would be crucial to develop reliable recommendations for resource-poor farmers. In developing countries, the need for collective action in the farming community was identified as a key obstacle to improve the adoption rates of integrated pest management practices (Parsa *et al*., 2014). Studies on information diffusion and adoption of agricultural innovations have indicated the critical and interdependent roles played by extension services and farmer social networks for establishing effective communication channels (Garrett, 2012; Genius *et al*., 2014). Research on social modelling and the psychology of decision making, integrated with research on biotic, economic and environmental traits affecting seed degeneration, is thus much needed. Studies employing interdisciplinary diagnostic methods such as technography (see Table 2 for definition) to understand the contexts that determine the performance of a technology (Jansen & Vellema, 2011) are particularly relevant for degeneration management.

Improved insights into epidemiology of degeneration and interrelationships between risk factors

Understanding the epidemiology of year-round disease maintenance in seed is useful for better management of seed degeneration. Mixed infections of viruses are commonly observed in potato seed obtained via the informal seed system (Gildemacher *et al*., 2009). Understanding species- and strain-specific factors, especially in relation to host resistance and environmental cues, is important to tailor a subset of highly effective management practices for the predominant causes of seed degeneration in a region. The RTB project on degeneration mentioned above has, as one of its objectives, the development of models to predict degeneration that include the effects of host resistance and environmental factors. Such models would aid understanding of the interrelated risk factors of seed health and the development of agricultural interventions and decision support tools at the scale of individual farmers or communities. Using such decision support systems, local governmental and non-governmental extension agencies would be able to provide practical recommendations to growers to implement the integrated seed health strategy.

Understanding the impact of climate change on potato seed degeneration

In a recent study by van der Waals *et al*. (2013), the aphid population in specific agroecosystems in South Africa was predicted to increase by 2050. This in turn could increase outbreaks of PVY and PLRV epidemics. Virus replication and movement rates can be affected by climate change (Canto *et al*., 2009), and potato tuber infection is temperature sensitive, with increased susceptibility in warmer temperatures (Bertschinger *et al*., 1995b). Together with new and emerging tuberborne infections, these studies suggest that degeneration of potato is likely to become a greater challenge in the coming decades, with predicted increasing temperatures.

Using positive deviance to improve management of potato seed production

In communities of people struggling with a common health or food production problem, there are sometimes people who succeed, even though they do not have obvious access to additional resources outside those available to everyone in the community (Marsh *et al*., 2004). These creative individuals hold the solution to using locally available resources to manage a complex problem and should be sought out by those hoping to understand how to better address the challenge. This approach, known as ‘positive deviance’, has been used to improve health, nutrition and education in multiple communities (Marsh *et al*., 2004). It has rarely been used to deliberately address agricultural challenges (Oyarzun *et al*., 2013), even though extension workers often identify successful farms. The integrated seed health strategy is essentially a public health approach to potato production, encouraging farmers to use multiple approaches to address a complex problem. Educational tools (that use the same vocabulary, metaphors and concepts) used for animal and human health may be employed to address multiple types of health problems, including potato seed health.

Understanding how the combination of ‘business ecosystem’ and agroecosystem influences the success of seed degeneration management

A ‘business ecosystem’ includes a set of businesses and their interactions necessary for any given business to be successful (Iansiti & Levien, 2004). Many applications of the concept can be found in the IT industry, where compatibilities and synergies among products are needed for businesses to succeed. The set of businesses and stakeholders in seed systems can be thought of as a business ecosystem, where there is a need for greater understanding of the environmental and socioeconomic conditions necessary for successful implementation of the integrated seed health strategy. Research should address how to identify and support the conditions that make management components viable. Certified seed plantings are vulnerable to rapid infection from other sources, so management choices of neighbouring farmers and their seed suppliers will influence the success of any given farmer. Agroecological conditions in tropical countries may also be more favourable to inoculum build-up. Given this, what local pathogen population threshold would make certified seed systems viable, and what system components are necessary to keep populations below the threshold? Similarly, implementation of techniques such as plant selection requires that farmers be familiar with disease symptoms and have labour available. What system components are necessary to make such on-farm management successful? Ultimately it will also be important to understand how different seed systems are more or less resilient to different shocks, such as the introduction of new pathogens or unusually disease/pest-conducive weather conditions (Folke, 2006).

Many interrelated factors in the biology, socioeconomics, and policy of potato seed play crucial roles in the effective management of seed degeneration in potato. Some challenges such as the unpredictability of seed degeneration in on-farm seed material, unavailability of resistant varieties, and lack of approaches to objectively integrate management strategies across agroecological zones, emphasize the need for more research initiatives. Other challenges, such as the uptake of seed regeneration methods (e.g. plant selection), deployment of resistant varieties, and establishment of profitable seed production systems, require translational research, improved farmer education and research into the socioeconomics and behavioural economics of using certified seed. Yet other challenges, such as developing realistic tolerance thresholds in certified seed systems, and establishing a research and development agenda that focuses on the integrated seed health strategy, require improved policy and regulations for seed degeneration management. Such a multipronged approach is likely to be successful in managing this devastating problem for potato producers in many developing countries.

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