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Variety and on-farm seed management practices affect potato seed degeneration in the tropical highlands of Ecuador

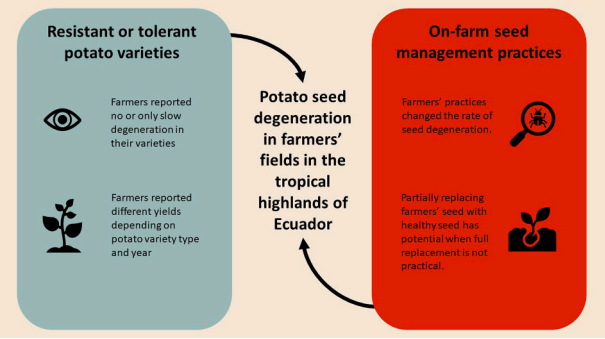
Israel Navarrete [a,b,c,d,*], Victoria López [e], Ross Borja [f], Pedro Oyarzún [f], Karen A. Garrett [g,h,i], Conny J.M. Almekinders [c,d], Yanru Xing [g,h,i], Paul C. Struik [b], Jorge L. Andrade-Piedra [d,j]

[a] International Potato Center, Quito, Ecuador
[b] Centre for Crop Systems Analysis, Wageningen University and Research, Wageningen, The Netherlands
[c] Knowledge, Technology and Innovation, Wageningen University and Research, Wageningen, The Netherlands
[d] CGIAR Research Program on Roots, Tubers and Bananas (RTB), Lima, Peru
[e] Instituto Nacional de Investigaciones Agropecuarias del Ecuador, Quito, Ecuador
[f] Ekorural, Quito, Ecuador
[g] Plant Pathology Department, University of Florida, Gainesville, FL, USA
[h] Food Systems Institute, University of Florida, Gainesville, FL, USA
[i] Emerging Pathogens Institute, University of Florida, Gainesville, FL, USA
[j] International Potato Center, Lima, Peru

HIGHLIGHTS

- This study combines results from farmer surveys, seed lots analysis, and the seedHealth model.
- Farmers in Ecuador report that their varieties do not degenerate or degenerate slowly.
- On-farm management increases or reduces seed degeneration depending on the cause.
- Partial seed replacement is a promising practice to manage seed degeneration.

GRAPHICAL ABSTRACT



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ABSTRACT

CONTEXT: Studies in the Andes have demonstrated that seed degeneration of potato occurred in experimental conditions, but was negligible in farmers' conditions. There are two hypotheses for this difference: (1) farmers cultivate resistant varieties, or (2) they use on-farm practices that can manage seed degeneration. Farmers may replace some of the seed saved from their fields with outside seed, but it is an open question what level of benefit farmers experience from partial replacement.
OBJECTIVES: The objective of this study was to investigate the role of the cultivated varieties, the on-farm seed management practices, and seed replacement in potato seed degeneration. Moreover, this study evaluated the potential effect of partial replacement of the farmers' seed lot each season with healthy seed, compared to less frequent nearly full replacement, in simulations.

* Corresponding author at: International Potato Center, Quito, Ecuador.
E-mail address: israelnavarrete2@gmail.com (I. Navarrete).

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METHODS: We surveyed farmers in the Cotopaxi province, Ecuador, in 2008, 2010, and 2018, and performed a study on the incidence of pathogens and pests in farmers' seed lots in 2018. We also evaluated the potential effects of the timing of replacement of farmers' seed lots by healthy seed to manage degeneration, applying the seedHealth model.
RESULTS AND CONCLUSIONS: We found that farmers experience no or only slow degeneration in their varieties. Analysing yield data reported by farmers to detect degeneration, we did not detect yield declines. The type of variety and year of data collection explained the variation in yield. These results seem to confirm the hypothesis that varieties cultivated in the Andes are resistant to the impact of seed degeneration on yield, and that seed degeneration depends on the agroecological conditions present within a cropping season or year. Because we did not find an impact on yield, we hypothesized that on-farm practices affect seed-borne pathogens and pests causing seed degeneration. We identified multiple on-farm practices playing a role in the process of seed degeneration: they either slowed down or accelerated this process depending on the seed-borne pathogen and pest causing seed degeneration. Our scenario analyses using the seedHealth model showed how replacing farmers' seed lots by healthy seed could usefully reduce seed degeneration compared to using the same amount of seed to periodically replace nearly all seed in a season. Our results showed that on-farm practices are also critical drivers in the process of seed degeneration.
SIGNIFICANCE: This study demonstrated the importance of considering on-farm seed management practices (i.e., use of cultivated varieties) to strengthen seed systems interventions aiming to manage potato seed degeneration. Additionally, this study showed the potential of partially replacing farmers' seed with healthy seed as an alternative when complete seed replacement is not an option.

1. Introduction

Potato (*Solanum tuberosum*) seed degeneration affects farmers' potato production in low-income countries. We define seed degeneration as the reduction in seed quality and yield due to the accumulation of pathogens and pests in/on the seed tubers (hereafter seeds) occurring when seed is recycled (i.e., propagated over consecutive cycles of on-farm multiplication) (Struik and Wiersema, 1999). Some examples of pathogens and pests that cause seed degeneration are Potato virus Y (PVY), *Ralstonia solanacearum* (causal agent of bacterial wilt), and *Globodera pallida* (commonly known as potato cyst nematode). Without proper management, these diseases and pests could accumulate in the farmers' seed lot and reduce seed quality. In the lowlands of Colombia, experiments showed that the percentage of seed infected with PVY could increase by 40% in one cycle of on-farm propagation (de Luque et al., 1991). Nevertheless, this increase in the percentage of infected seed depends on many factors including agroecological conditions (Bertschinger et al., 2017; Thomas-Sharma et al., 2016). These diseases and pests can also cause serious yield losses. For instance, PVY can cause losses of 0.18 t ha^{-1} on average for each 1% increase in incidence (Nolte et al., 2004); the Andean potato weevil (*Premnotrypes* sp.) can cause yield losses up to 100% (Kroschel et al., 2014). These examples provide an approximation of the impact of seed degeneration on farmers' fields. Therefore, it is necessary to identify management options for this problem.

Scientists participating in the CGIAR Research Program on Roots, Tubers and Bananas (RTB) proposed the Integrated Seed Health approach (ISH) and the use of the seedHealth model to improve the management of potato seed degeneration. The ISH is a framework that proposes the use of resistant varieties, seed replacement with certified or other high-quality seed, and on-farm seed practices (e.g., seed selection) to manage this problem (Kreuze et al., 2020; Thomas-Sharma et al., 2016). The use of resistant varieties has the potential to reduce the impact of seed degeneration on seed quality and yield (Salazar, 1996). When using the term "resistant varieties", we refer to varieties that are not only resistant (i.e., have ability to limit the pathogen and pest multiplication; Pagán and García-Arenal, 2020), but also tolerant (i.e., have the ability to withstand the negative impacts of infection or infestation; Pagán and García-Arenal, 2020). Different types of resistance exist as in the case of viruses: (1) resistance to virus accumulation, (2) resistance to virus movements within the plant, (3) hypersensitivity (i.e., pathogens are restricted to the area of inoculation visible by necrotic reactions), and (4) resistance to vectors (Barker and Dale, 2006; Salazar, 1996). Yet, the development of potato varieties resistant to viruses is slow (Kromann et al., 2014). Seed replacement aims to replace degenerated seed with certified or other high-quality seed. Unfortunately, seed replacement with certified seed is not a feasible option in low-income countries (Thomas-Sharma et al., 2016). On-farm seed management practices aim to reduce inoculum density and sources of inoculum. Examples of such practices are positive selection (i.e., selecting the best plants for seed mother plants; Gildemacher et al., 2011; Priegnitz et al., 2020), rogueing (i.e., removing diseased or affected plants; Broadbent et al., 1950), and the seed plot technique (i.e., small plot dedicated only to seed production; Bryan, 1983). The seedHealth model can contribute to understanding how host resistance, seed replacement and on-farm management practices affect seed degeneration, and to evaluating the performance of combinations of management practices using scenario analysis in different environments before establishing experiments (Andersen Onofre et al., 2021; Garrett and Xing, 2021; Thomas-Sharma et al., 2017). The combination of the ISH approach with the use of the seedHealth model could identify the effectiveness of practices to manage seed degeneration.

Potato seed degeneration continues to be poorly understood in the Andes of Ecuador. Recently, research indicated that agroecological conditions and number of cycles of on-farm propagation partially explained the accumulation of pests and diseases in/on the seed only under experimental conditions; but, under farmers' conditions, degeneration was negligible (Navarrete et al., 2021a). These contrasting results suggest that farmers are either using tolerant/resistant potato varieties or indirectly managing this problem with unidentified practices. The finding that approximately half of the farmers in the Andes of Ecuador do not observe seed degeneration (Navarrete et al., 2021b) indicates that both options are possible. The other half of the farmers in the Andes of Ecuador reported observing seed degeneration and claimed to replace their seed once it is degenerated, as a direct management practice. But, their seed replacement practices (e.g., purchasing seed) were similar to those reported by farmers who did not observe degeneration (Navarrete et al., 2021b). To the best of our knowledge, there are no studies that explore the effect of farmers' varieties and on-farm seed practices on seed degeneration in the Andes.

In the Andes, such studies should cope with the huge potato diversity. For example, in Ecuador there are between 350 and 450 varieties (Cuesta et al., 2005), in Peru between 2800 and 3300 varieties (de Haan and Rodriguez, 2016), and in Bolivia between 1000 and 1500 varieties (de Haan and Rodriguez, 2016). However, only a portion of these varieties are available in the market; in the central provinces of Ecuador, for instance, the number of varieties that are available in the market is only 17 (Hidalgo et al., 2011). Currently, it is presumed that

many of these varieties have a certain level of tolerance to potato seed degeneration caused by viruses (Forbes et al., 2020). This is because Andean potato varieties have genes conferring resistance or tolerance to different viruses such as PVY or Potato virus X (PVX) (Kreuze et al., 2020).

On the other hand, on-farm seed management practices could influence the presence and dissemination of diseases and pests causing degeneration (Andersen et al., 2019; Buddenhagen et al., 2017). Usually, planting starts in a field that was fallowed before (Arce et al., 2019; de Haan, 2009). Potato could be cultivated repeatedly in the same field or rotated with other crops such as barley, oats, legumes, or pasture (Arce et al., 2019). From the harvest, farmers separate tubers as planting material for the next season (Kromann et al., 2016). This practice of saving seed could occur for several consecutive years (Crissman and Uquillas, 1989) suggesting the potential for seed degeneration. It is presumed that the effectiveness of this seed selection practice could be inversely related to the market price of ware potato (Velásquez, 2006). When ware potato prices are low, farmers might select bigger (~ 60 g) and healthier seed tubers; whereas when there is a high price, they might keep smaller (< 60 g) and less healthy tubers (Velásquez, 2006). If farmers want to replace their seed lot entirely or partially, they could use different practices such as selecting seed from *ración* (i.e., in-kind payment in the form of potatoes received when assisting other farmers during the harvest), selecting seed from potatoes obtained as gifts, or purchasing seed mainly from the markets (de Haan, 2009). When farmers replace part of their seed lot with seed from external sources, for example from *ración* or from a gift, potato seed degeneration could increase or decrease depending on the health level of the seed. Yet, the effect of replacing only a percentage of seed across seasons of on-farm propagation remains to be investigated. One approach to evaluating the benefit of regular partial seed replacement is to compare it to less frequent consolidated replacement. That is, what are the expected benefits of using the same amount of disease-free seed for (a) partial replacement every season, versus (b) complete replacement but less frequently? The situation could be more unpredictable due to the farmers' storage conditions, such as keeping potatoes in net bags (de Haan and Thiele, 2003), which could contribute to the development and spread of diseases, or the use of herbs on top of the net bags as pest repellent thus reducing seed degeneration (Love et al., 2020).

Hence, the research questions in this paper are: (1) what is the role of the cultivated varieties, seed replacement, and the on-farm seed management practices in potato seed degeneration? and (2) what is the potential effect of replacing part of the farmers' seed lot by healthy seed (i.e., seed that have an incidence of pathogens and pest damage below an established threshold) every season, relative to the benefit of using the same total amount of healthy seed for periodic (not every season) complete replacement during on-farm propagation? To answer these research questions, we first describe the practices that potentially manage seed degeneration: use of resistant varieties (expressed as farmers' experienced varietal reaction to seed degeneration), seed replacement, and on-farm seed management practices (e.g., seed selection or using fallow periods). Then, we describe the effect of these practices on seed degeneration expressed as the variation in yield and the variation in the presence of seed-borne pathogens and pests in farmers' seed lots. Next, we present the likely outcomes of scenarios for replacing a percentage of the farmers' seed lots with healthy seed using the seedHealth model. We expect that the results in this paper will motivate a discussion about the role of cultivated varieties and on-farm seed management practices to improve the design and implementation of seed interventions.

2. Methodology

We used the ISH approach and the seedHealth model to understand the role of: (1) the cultivated varieties (using the farmers' experienced reaction of the variety), (2) the seed replacement (evaluated based on the number of cycles of on-farm propagation, no distinction was made on whether the seed was certified or not), and (3) other on-farm seed practices in the management of seed degeneration in the tropical highlands of Ecuador. For this, we surveyed farmers in the province of Cotopaxi, Ecuador, in 2008, 2010, and 2018 (Fig. 1). We collected seed from farmers surveyed in 2018 to evaluate the incidence of seed infected with viruses, pathogens other than viruses (e.g., *Rhizoctonia solani*), and with insect damage. With these data, we parameterized the seedHealth model (Garrett and Xing, 2021; Thomas-Sharma et al., 2017) to understand the effect of partitioning of a volume of healthy seed across time during on-farm propagation, as it is likely to contribute to managing seed degeneration.

2.1. Context of the studies

We performed this research in the province of Cotopaxi in the central highlands of Ecuador. This province is characterized by an intervalley and the western and eastern highlands (Fig. 1). The main cultivated crops in the Andean region of the province are broccoli (*Brassica oleracea*), maize (*Zea mays*), and potato (Ministerio de Agricultura y Ganadería, 2020a). In 2020, this province produced 47,598 tons of potato which accounted for 11% of the national production (Ministerio de Agricultura y Ganadería, 2020a). Potato is also one of the most important income sources for farmers despite the fact that most farmers (81%) plant this crop in 1 ha or less (Ministerio de Agricultura y Ganadería, 2018). These farmers have on average 7 years of school education, and rarely, they are involved in training events (Ministerio de Agricultura y Ganadería, 2018). Moreover, the productivity of the province of Cotopaxi is one of the lowest in the country (average = 10.3 t ha^{-1}; national average = 16.3 t ha^{-1}; year 2020; Ministerio de Agricultura y Ganadería, 2020b). Potentially, this low value is associated with the low access to resources. For example, it is estimated that 63% of the farmers use machinery mainly to prepare the soil for planting, and only 41% of the farmers have access to irrigation (Ministerio de Agricultura y Ganadería, 2018). In 2019, only 5% of the farmers had access to certified seed (Ministerio de Agricultura y Ganadería, 2019). It is also estimated that farmers apply 39 kg ha^{-1} of nitrogen, 99 kg ha^{-1} of phosphorus, and 47 kg ha^{-1} of potassium (Ministerio de Agricultura y Ganadería, 2019). These amounts of nutrients are low if they are compared with the general recommendation for Ecuador: 100 kg ha^{-1} of nitrogen, 200 kg ha^{-1} of phosphorus, and 60 kg ha^{-1} of potassium for soils containing intermediate levels of these elements (recommendations to achieve 30 to 50 t ha^{-1}; Oyarzún et al., 2002). The main concerns for most potato farmers in this province are pests and diseases affecting the crop. Particularly, the impacts associated with purple top – a recent phytosanitary problem in Ecuador (Castillo, 2020) – and the Andean weevil are considered serious (Ministerio de Agricultura y Ganadería, 2020b).

2.2. Farmers' surveys

In 2008 and 2010, we surveyed 58 and 59 households in different locations in the province of Cotopaxi (Fig. 1), respectively. Farmers surveyed represented a complete census of the participants in a previous project. This project supported smallholder indigenous farmers that had high levels of agrobiodiversity in their fields. Farmers were asked to list the potato varieties in their seed lots. Because farmers plant multiple varieties, we obtained the information for 153 seed lots in 2008 and 114 in 2010. For each variety, we asked: (1) how long were farmers growing those varieties, (2) the number of bags of 45.45 kg planted (known as *quintal* in Ecuador) in the previous season, and (3) the resulting number of bags harvested in the previous season. The area planted was derived dividing the number of bags of 45.45 kg planted by 34 which is the approximate number of bags that farmers plant per hectare (Albornoz, 1968). Total productivity was obtained by transforming the number harvested to tons. Yield was estimated by dividing the total productivity by the area planted. Raw data are available upon request to the first

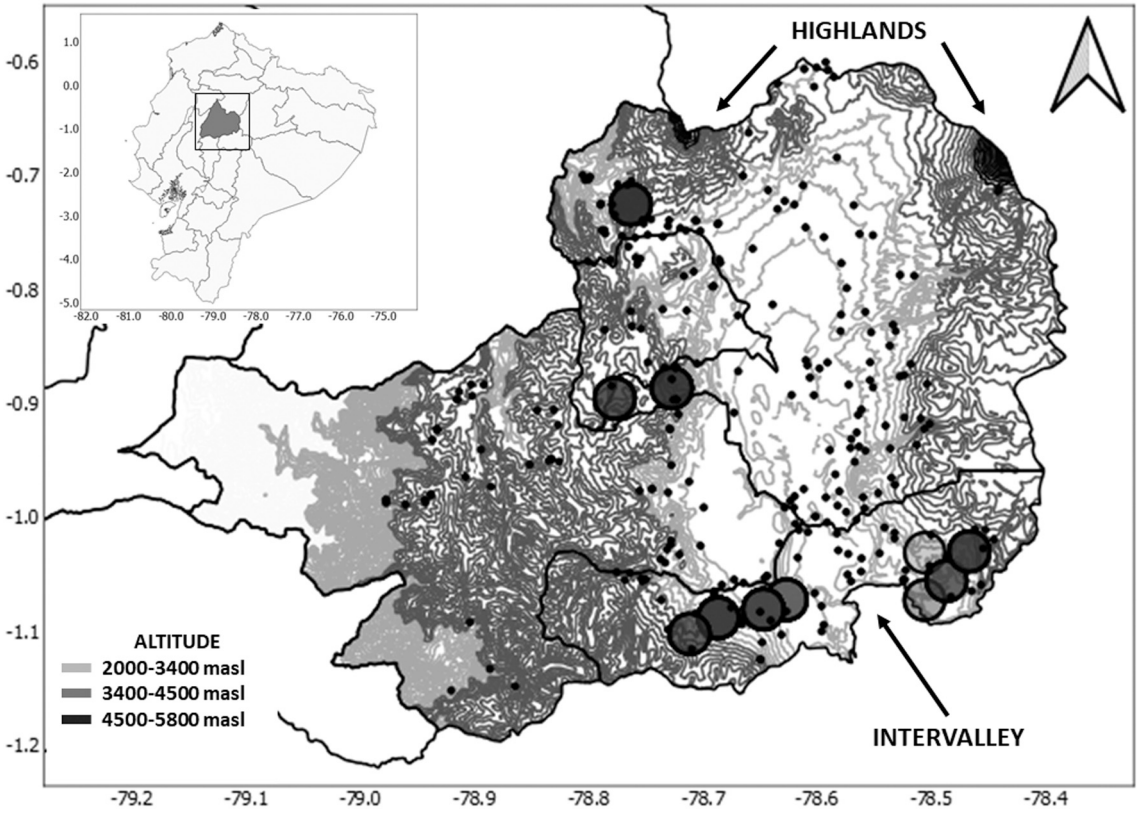

Fig. 1. Map of the province of Cotopaxi. The map in the upper left corner represents Ecuador, and the dark grey area is the location of the province of Cotopaxi in the country. The enlarged map shows the main potato production cantons (covered by the altitude contour lines), the location of the intervalley and of the highlands in the province. Circles represent areas surveyed in 2008 and 2010. Dots show the geographical locations of the surveys during 2018.

author.

In 2018, we randomly surveyed 260 households at the beginning of the planting season in the province of Cotopaxi (Fig. 1) as reported by Navarrete et al. (2021a). Briefly, we randomized the surveys by overlapping the altitude map of the province of Cotopaxi over a map created with 260 square grids. We surveyed a farmer willing to answer our questions close to the center of each square grid. The questionnaire used in this survey was a modification of the Rural Household Multi-Indicator Survey (RHoMIS) (Hammond et al., 2017), including the questions considered in 2008 and 2010. Hence, we collected the information for 589 seed lots. We also asked whether farmers experienced seed degeneration or, in farmers terms, if the *seed got tired*. Farmers that replied affirmatively were asked, for each variety, to rank the rate at which their varieties degenerated by selecting from the following options: no degeneration, slow degeneration, or fast degeneration. In addition, we included questions related to on-farm seed management practices. Yield was estimated as described above for the surveys in 2008 and 2010. Later, the data was classified according to the agroecological conditions identified by Navarrete et al. (2021a) in the province: the intervalley and the highlands (Fig. 1). Raw data for 2018 is available in Navarrete et al. (2018).

2.3. Seed lot analysis

During the farmers' survey in 2018, we collected a sample of 10 seed tubers per seed lot to estimate the incidence of seed-borne diseases and pests as reported by Navarrete et al. (2021a). Briefly, the seed samples collected were transported to the International Potato Center research station in Quito (CIP-Quito). Upon arrival, we assessed the incidence of bacterial and fungal diseases and insect damage on each of the seed tubers (James, 1971). Seed tubers were either planted into 5-L pots or allowed to sprout before planting. When plants were approximately 15–20 cm tall, we collected leaf samples and performed DAS-ELISAs for virus detection (CIP, 2007). The samples were screened for the following viruses: PVX, Potato virus S (PVS), PVY, Potato leaf roll virus (PLRV), Andean potato mosaic virus (APMoV), and Andean potato latent virus (APLV). With this information, we estimated the percentage of seed tubers infected with viruses, the percentage of seed tubers infected with pathogens other than viruses (referred to as *other pathogens* in the rest of the manuscript), and the percentage of seed tubers with insect damage. Raw data can be found in Navarrete et al. (2019).

2.4. Statistical data analysis

Description of the practices: Experienced reactions of varieties to seed degeneration, seed replacement, and on-farm management practices. We used descriptive statistics, Pearson's Chi-Square tests, and an ordinal logistic regression to evaluate the frequency of and the differences in the experienced varietal reactions and seed replacement between the intervalley and the highlands of Cotopaxi. This analysis was disaggregated between variety types: improved and native varieties. The frequency of the on-farm management practices was estimated using descriptive statistics. We used Pearson's Chi-Square tests to evaluate the difference in the percentage of farmers implementing the practices between the intervalley and the highlands.

Effect of variety type and seed replacement on yield variation. To estimate the effect of the variety type and seed replacement on yield (as a proxy for seed degeneration), we implemented a hierarchical linear model (Eq. 1). We used the "lmer" function in the R package "lme4" (Bates et al., 2015). In this model, yield was the response variable and the number of cycles of on-farm propagation was the fixed effect. The variety type, year of data collection, and agroecological conditions were included in the model as random effects.

$$\text{Yield} = \text{Cycles}_i + \text{Variety}_j + \text{Year}_k + \text{Agroecological conditions}_l + \varepsilon_{ijkl}$$

Eq. (1). Regression to estimate the variation in yield across on-farm propagation cycles, the type of variety, the year of data collection and agroecological conditions.

Effect of on-farm management practices on the presence of viruses, insect damages and other pathogens. We estimated the effect of on-farm management practices identified during 2018 on: (1) the percentage of seed infected with viruses, (2) the percentage of seed infected with other pathogens, and (3) the percentage of seed with insect damages. Effects were estimated using regression trees with the "rpart" function in the R package "rpart" (Therneau et al., 2019). We did not perform a regression tree between on-farm management practices and yield because it was not going to provide results associated with seed degeneration.

2.5. Understanding the effects on seed degeneration of replacing only a fraction of seed with healthy seed

We used the seedHealth model in R (Garrett and Xing, 2021; Thomas-Sharma et al., 2017) to understand the likely effect of partitioning use of a fixed volume of healthy seed across time, because farmers in this system more typically only use a portion of outside seed. If only some outside healthy seed can be obtained, how well does using a share of outside seed every year perform compared to consolidating use of outside seed for more substantial replacement less frequently? We simulated replacement of part of the farmers' seed lots by healthy seed on the portion of infected/infested plants at the end of the cycle across 12 cycles of on-farm propagation. We defined four scenarios for seed replacement (Table 1). In the first scenario, we simulated the potential effect of farmers' multiplying their seed without any replacement, for reference. The three other scenarios each had the same overall amount of healthy seed added to the system, but distributed differently across time. In the second scenario, we simulated the effect of replacing a low proportion (30%) of the seed lot by healthy seed in every cycle. In the third scenario, we simulated the effect of replacing a medium proportion (60%) of the seed lot by healthy seed once every two cycles (Table 1). In the fourth scenario, we simulated the effect of replacing a high proportion (90%) of the seed lot by healthy seed, but only once every three cycles (Table 1). We did not evaluate seed replacement with 100% of healthy seed because that usually occurs when smallholder farmers lost their seed due to frost, hail or drought rather than because of seed degeneration (Crissman and Uquillas, 1989). We also did not evaluate the impact of agroecological conditions because it was recently demonstrated that their effect is negligible on potato seed degeneration under farmers' conditions in the tropical highlands of Ecuador (Navarrete et al., 2021a). We evaluated these four replacement scenarios under low and high external inoculum (i.e., local disease or pest pressure) conditions. Hence, in total, we evaluated eight cases in the seedHealth model (four scenarios under two external inoculum levels each). Each case was evaluated in 400 realizations to capture average outcomes across stochastic simulations. We compared the results for each of the scenarios in terms of the average percentage of infected/infested plants due to seed degeneration. The values for the other parameters needed to run the seedHealth model are in the Supplementary information 1 and the code and output of the model are in Supplementary information 2.

Table 1
Scenarios for seed replacement during six cycles of on-farm propagation (out of the 12 simulated with the seedHealth model).

Scenario	Farmers' seed lot replaced by healthy seed (%)					
	Cycle 1	Cycle 2	Cycle 3	Cycle 4	Cycle 5	Cycle 6
1. No replacement	0	0	0	0	0	0
2. Low proportion – every cycle	30	30	30	30	30	30
3. Medium proportion – once every 2 cycles	60	0	60	0	60	0
4. High proportion – once every 3 cycles	90	0	0	90	0	0

3. Results

3.1. Characterization of local practices that potentially manage degeneration

Experienced varietal reactions to seed degeneration: Our analysis of data from 2008, 2010, and 2018 revealed that there were 65 potato varieties cultivated by smallholder farmers in the province of Cotopaxi (Supplementary information 3). Sixteen of them were improved varieties, or genotypes that escaped from field experiments (fourth author personal observation). Along with these improved varieties, we found 49 native potato varieties cultivated in the province. The number of varieties grown was greater among farmers in the highlands (57 varieties) than among farmers in the intervalley (28 varieties) ($p < 0.001$). Overall, farmers had on average 2.4 potato varieties (standard deviation [sd] = 1.3). The most common varieties were Super chola (improved variety; planted by 25.1% of farmers in 2018), Leona blanca (native variety; planted by 12.5% of farmers in 2018), Leona negra (native variety; planted by 11.7% of farmers in 2018), and Chaucha amarilla (native variety; planted by 11.1% of farmers in 2018).

Farmers had different perceptions about the reactions of their varieties to seed degeneration. A large percentage of farmers (84.1%) reported that their seed lots did not degenerate or degenerated slowly. These perceptions did not change when comparing the type of variety or the agroecological conditions ($p > 0.6$) (Fig. 2A). The percentage of farmers perceiving that their seed lots did not degenerate (47.2%) or degenerated slowly (36.9%) was similar ($p = 0.06$), and the percentage of farmers perceiving that their seed lot degenerated rapidly was much lower (15.9%). The percentage of farmers perceiving that their seed lots did not degenerate or degenerated slowly was greater than the percentage of farmers perceiving that their seed lots degenerated rapidly ($p < 0.001$) (Fig. 2A).

Seed replacement. Our results showed that farmers replaced their seed lots after different numbers of cycles (years) of on-farm propagation (Fig. 2B). However, seed replacement rates depended on the interaction between the agroecological conditions and the type of variety ($p = 0.02$). In the highlands, seed replacement rates were different for improved and native varieties ($p < 0.001$). Here, there was a small and similar percentage of seed lots of improved and native varieties replaced before 1 year: 5.2 and 3.2%, respectively ($p = 0.42$). Moreover, we observed that there was a higher percentage of improved varieties (42.2%) replaced between 1 and 3 years in comparison with the percentage of seed lots of native varieties (26.3%; $p < 0.001$). There were similar percentages of seed lots of both types of varieties replaced between 3 and 10 years (average 31.2%; $p = 1$). We also found that there was a smaller percentage of seed lots of improved varieties that were replaced after 10 years (21.4%) in comparison with the percentage of seed lots of native varieties (39.2%; $p < 0.001$) (Fig. 2B). In the intervalley, on the contrary, no differences were identified between the types of varieties and the seed replacement rates (all comparisons had a $p > 0.05$) (Fig. 2B).

On-farm seed management practices. We identified 36 seed practices with the potential to contribute to the management of seed degeneration. The most common ones were: (1) waiting for the seed to sprout (97% of farmers), (2) giving potatoes as a gift (94%), (3) selecting seed at harvest (94%), (4) tilling the soil with machine traction (95%), and (5) storing potatoes in polypropylene bags (89% of farmers) (Fig. 3). Similar percentages of farmers implemented these practices in the intervalley and in the highlands ($p > 0.05$). Besides, we identified

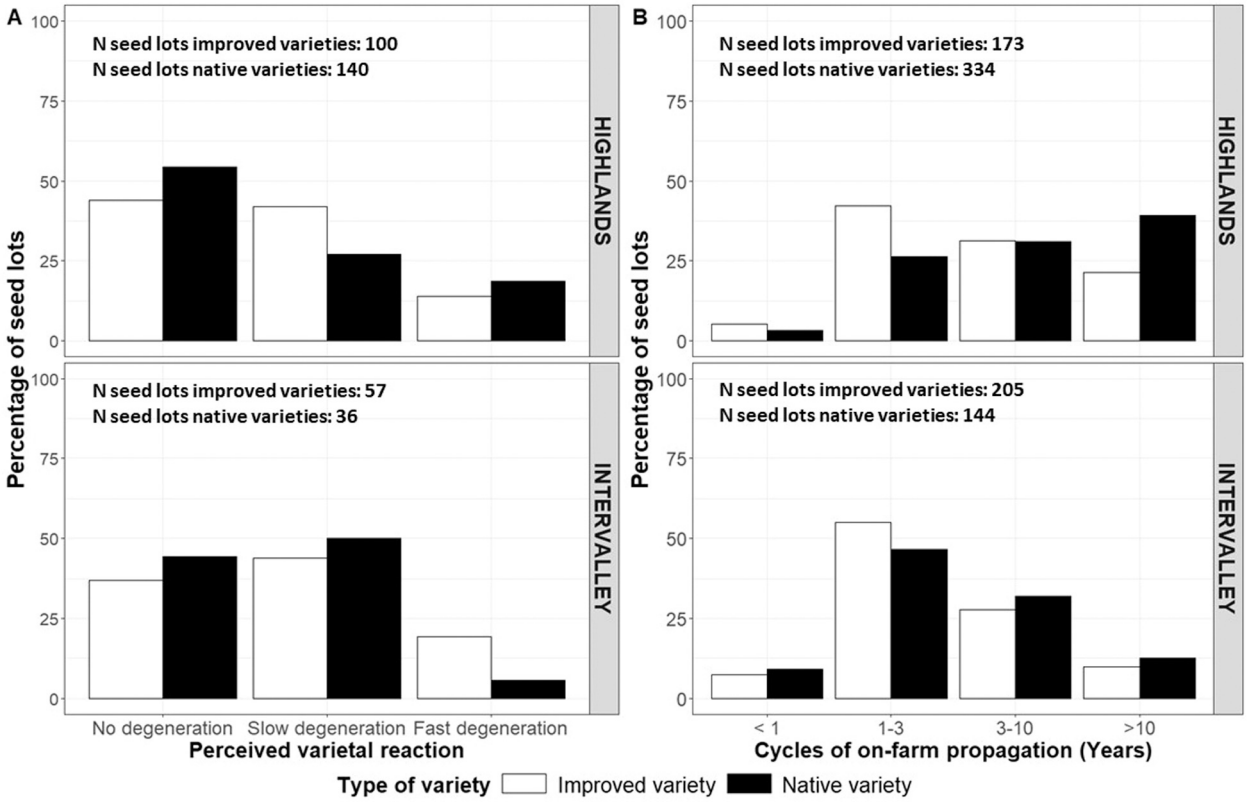

Fig. 2. Farmers' experienced varietal reaction to seed degeneration (A) and seed lot replacement (B) in two agroecological conditions (highlands and intervalley) in the province of Cotopaxi in Ecuador. Fig. 2A shows data collected in 2018 from farmers who observed seed degeneration. Fig. 2B shows data collected in 2008, 2010, and 2018.

multiple practices that were implemented more frequently in the intervalley than in the highlands (Fig. 3). For example, we found that more farmers applied irrigation in the intervalley (66.7%) than in the highlands (28.3%) ($p = 0.01$). Disinfection of the seed was also implemented more frequently by farmers in the intervalley (54.6%) than by farmers in the highlands (32.9%) ($p < 0.001$). We found that there was a larger percentage of farmers that prefer the seed produced at a different altitude location as starting material in the intervalley (46.3%) than in the highlands (31.6%; $p = 0.02$) (Fig. 3). There were also other practices more common in the highlands than in the intervalley (Fig. 3). Planting consecutively potato in the same field was one of the practices that was implemented by more farmers in the highlands (57.9%) than in the intervalley (43.5%) ($p = 0.03$). Receiving *ración* and fallowing potato plots for more than one year were other examples of practices implemented by more farmers in the highlands than in the intervalley (Fig. 3). We identified practices that were barely implemented such as rogueing or planting a seed plot (also known as seed plot technique) (Fig. 3).

3.2. Effect of improved and native varieties on yield variability over consecutive cycles of on-farm propagation

Our hierarchical model (Eq. 1) showed that the type of variety and the year of data collection explained part of the variation in yield (Fig. 4). In general, we found that improved varieties had higher yield (mean = 15.3 t ha^{-1}, sd = 11.8) than native varieties (mean = 12.9 t ha^{-1}, sd = 11.1) ($p < 0.01$) (Fig. 4). On the other hand, the model revealed that the yields reported during 2008 (mean = 9.3 t ha^{-1}, sd = 7.2) were the lowest of the three years of data collection ($p < 0.01$). Additionally, we found that the yields reported in 2010 were the highest (mean = 16.9 t ha^{-1}, sd = 8.2) of three years of data collection, but these were similar to the yields reported in 2018 (mean = 14.3 t ha^{-1}, sd = 12.2) ($p = 0.15$) (Fig. 4). The yield reported by farmers in each of the years of data collection was close to the national average (Fig. 4). Our model also showed that yield variation was not associated with the agroecological conditions and the cycles of on-farm propagation ($p_{agroecological\ conditions} = 1$, all comparisons for cycles were $p > 0.05$, data not shown).

3.3. On-farm seed management practices affecting the variability of seed infected with viruses, other pathogens, and seed with insect damage

Seed infected with viruses. Our results showed that three practices influenced the percentage of seed infected with viruses in the farmers' seed lots: (1) preferring the seed produced at a different altitude location as planting material, (2) receiving potato as a gift, and (3) selecting seed differently when ware potato price was low (Fig. 5A). Our results showed that farmers who prefered the seed produced at a different altitude location had a seed lot with a lower percentage of seed infected with viruses (estimated mean = 61%, data not shown) than when not having this preference (estimated mean = 73%, data not shown). From the farmers who prefered the seed produced at a different altitude location, those who did not receive potato as a gift had a lower percentage of seed infected with viruses (estimated mean = 44%) than those who received potato as gifts (estimated mean = 66%). On the other hand, we observed that farmers who did not prefer the seed produced at a different altitude location and performed a different seed selection when the price of ware potato was low had seed lots with a lower percentage of seed infected with viruses (estimated mean = 19%) than those who did not select the seed differently when the price was low (estimated mean = 74%) (Fig. 5A).

Seed infected with other pathogens. Four practices influenced the percentage of other pathogens in farmers' seed lots: the fallow period between potato plantings, the selection of seed when ware potato prices were high, receiving potato as gift, and preferring the seed produced at a

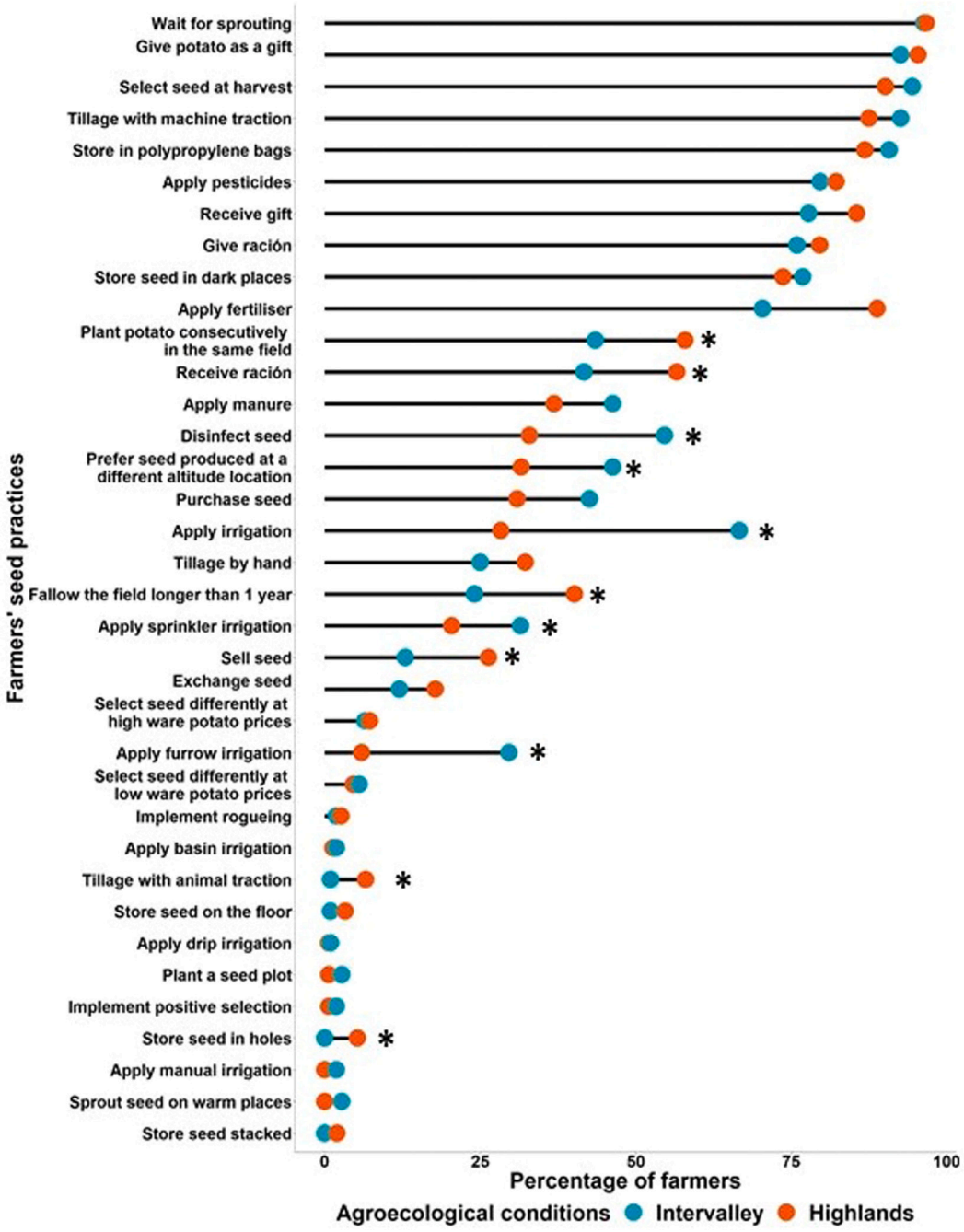

Fig. 3. Farmers' seed management practices identified in the tropical highlands of Ecuador. Asterisks identify which practices were implemented by different percentages of farmers in the two types of agroecological zones according to the Pearson's Chi-Square tests.

different altitude location as planting material (Fig. 5B). The fallow period between potato plantings was the most influential factor to determine the percentage of other pathogens in the farmers' seed lots. Farmers who had a fallow period between potato plantings of 2.5 years or more had a lower percentage of seed infected with other pathogens in their seed lots (estimated mean = 26%) (Fig. 5B) than farmers who had shorter fallow periods (estimated mean = 35%, data not shown). From the farmers who had a fallow period shorter than 2.5 years, those who performed a different seed selection when the ware potato price was high had a lower percentage of seed infected with other pathogens (estimated mean = 22%) (Fig. 5B) than those who did not select differently (estimated mean = 36%, data not shown). From the farmers who did not select differently, those who also did not receive potato as a gift had a lower percentage of seed infected with other pathogens (estimated mean = 30%) (Fig. 5B) than those who received potato as a gift (estimated mean = 38%, data not shown). From the farmers who received potato as a gift and implemented a fallow period longer than or equal to 0.85 years had a lower percentage of seed infected with other pathogens (estimated mean = 36%) (Fig. 5B) than when implementing shorter fallow periods (estimated mean = 44%, data not shown). Finally, the seed lots of the farmers who had fallow periods shorter than 0.85 years and belonged to farmers who prefered the seed produced at a different altitude location had a larger percentage of seed infected with other pathogens (estimated mean = 56%) than those who did not have this preference (estimated mean = 34%) (Fig. 5B).

Seed with insect damage. Four on-farm management seed practices influenced the percentage of seed with insect damage in the farmers' seed lots. These were the multiplication of seed during multiple cycles of on-

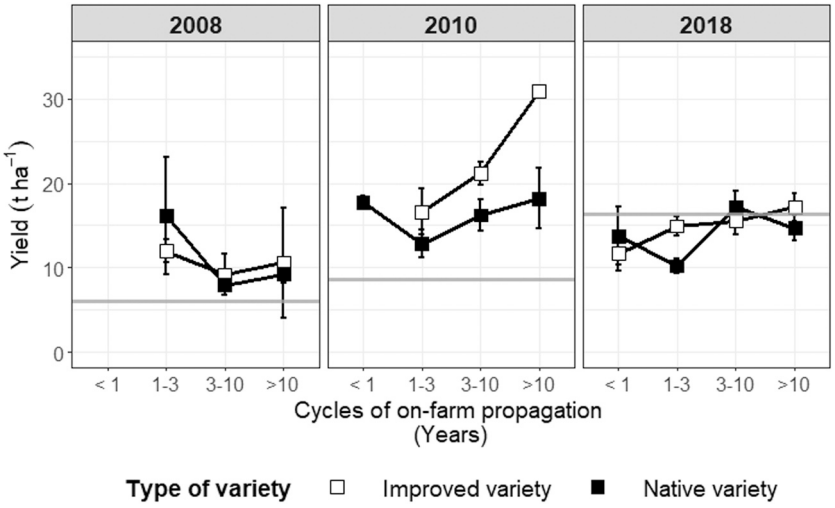

Fig. 4. Effect of improved and native varieties on yield variability as an expression of seed degeneration as recalled by farmers. Grey horizontal lines represent the average national yield of potato in each of the years of data collection. The national yield of 2008 comes from FAO (2021), and the national yields of 2010 and 2018 come from Ministerio de Agricultura y Ganadería (2020a).

farm propagation, selecting seed from *ración*, planting potato consecutively in the same field, and receiving *ración* (Fig. 6). More cycles of on-farm propagation led to a lower percentage of seed with insect damage. Seed lots with more than 3 years of on-farm propagation were estimated to have 54% of seed with insect damage (data not shown) while seed lots propagated for less than or equal to 3 years were estimated to have 65% of seed with insect damage (data not shown). When seed lots were propagated for more than 3 years, farmers that never or rarely selected the seed from *ración* had a lower percentage of seed with insect damage (52%) than those farmers who often or always selected seed from *ración* (73%) (Fig. 6). Among the farmers who propagated their seed lots for less than or equal to 3 years, those who planted potato consecutively had a lower percentage of seed with insect damage (58%) than those who did not plant potatoes consecutively (71%, data not shown). The farmers who did not plant potato consecutively and did not receive *ración* had a lower percentage of seed with insect damage (63%) than the same ones receiving *ración* (81%) (Fig. 6).

3.4. Understanding the effects on seed degeneration of replacing only a fraction of seed with healthy seed

In the scenario analyses using the seedHealth model, the comparison of the mean percentage of infected/infested plants at the end of each cycle to the null scenario without replacement of healthy seed, gives the relative benefit of seed replacement scenarios across the multiple cycles of on-farm propagation (Fig. 7A and B). In the scenario without replacement with healthy seed, the mean percentage of infected/infested plants at the end of each cycle was 97% (sd = 7) compared to 65% (sd = 29) in the scenarios of replacing seed. The level of external inoculum played an important role in seed degeneration (Fig. 7A and B). Scenarios with low external inoculum had a lower mean percentage of infected/infested plants at the end of each cycle (mean = 50%, sd = 24) than scenarios with high external inoculum (mean = 94%, sd = 13). Replacing lower percentages more frequently was not as effective as replacing higher percentages less frequently using the same total amount of seed (Fig. 7A and B). For example, in the scenarios where a medium proportion of the farmers' seed lot was replaced by healthy seed every other cycle, there was an average reduction of 18% under low external inoculum and 7% under high external inoculum on the mean percentage of infected/infested plants in the cycle of replacement. In contrast, in the cycles where a high proportion of the farmers' seed lot was replaced by healthy seed every three cycles, there was an average reduction of 28% under low external inoculum and 26% under high external inoculum on the mean percentage of infected/infested plants in the cycle of replacement. When seed cannot be obtained to replace a high proportion at the same time, replacing a lower proportion regularly still provided over half the benefit under low external inoculum and around a third of the benefit under high external inoculum, under the assumptions of the seedHealth model.

4. Discussion

In this article, we aimed to understand the role of potato varieties cultivated, seed replacement, and on-farm seed management practices on potato seed degeneration with smallholder farmers in the tropical highlands of Ecuador. Our main results showed that potato varieties cultivated in the province of Cotopaxi were reported by most farmers to be varieties that did not degenerate or degenerated slowly. We found that the seed lots of improved and native varieties were replaced after different numbers of cycles of on-farm propagation depending on the agroecological conditions. Our statistical analysis did not find evidence for differences in reduction in yield associated with seed degeneration for either improved or native varieties. This finding suggests that cultivated potato varieties in the Andes are resistant to the impact of seed degeneration on yield. Moreover, our results suggest that the impact of seed degeneration on yield, at least in the Andean context, is influenced by the agroecological conditions prevailing during the cropping season. We also investigated the role of on-farm practices on seed degeneration because these practices could be implicitly influencing seed-borne pathogens and pests, and could consequently hamper the detection of yield losses associated with seed degeneration. Thus, we registered 36 practices that have the potential to manage or accelerate the process of seed degeneration, or both, depending on the seed-borne pathogen and pest. Our modelling analysis indicated how replacing part of farmers' seed lots by healthy seed could contribute to managing seed degeneration, where even lower levels of replacement distributed across cycles provide a share of the benefit of more complete replacement. We discuss our results using the ISH approach and the seedHealth model.

4.1. Varietal reactions to seed degeneration, seed replacement, and portfolio of seed management practices

Farmers mainly experienced that their potato varieties did not degenerate or degenerated slowly (Fig. 2A). This perception did not change depending on the agroecological conditions. All together, these results add evidence supporting the existing hypothesis that Andean

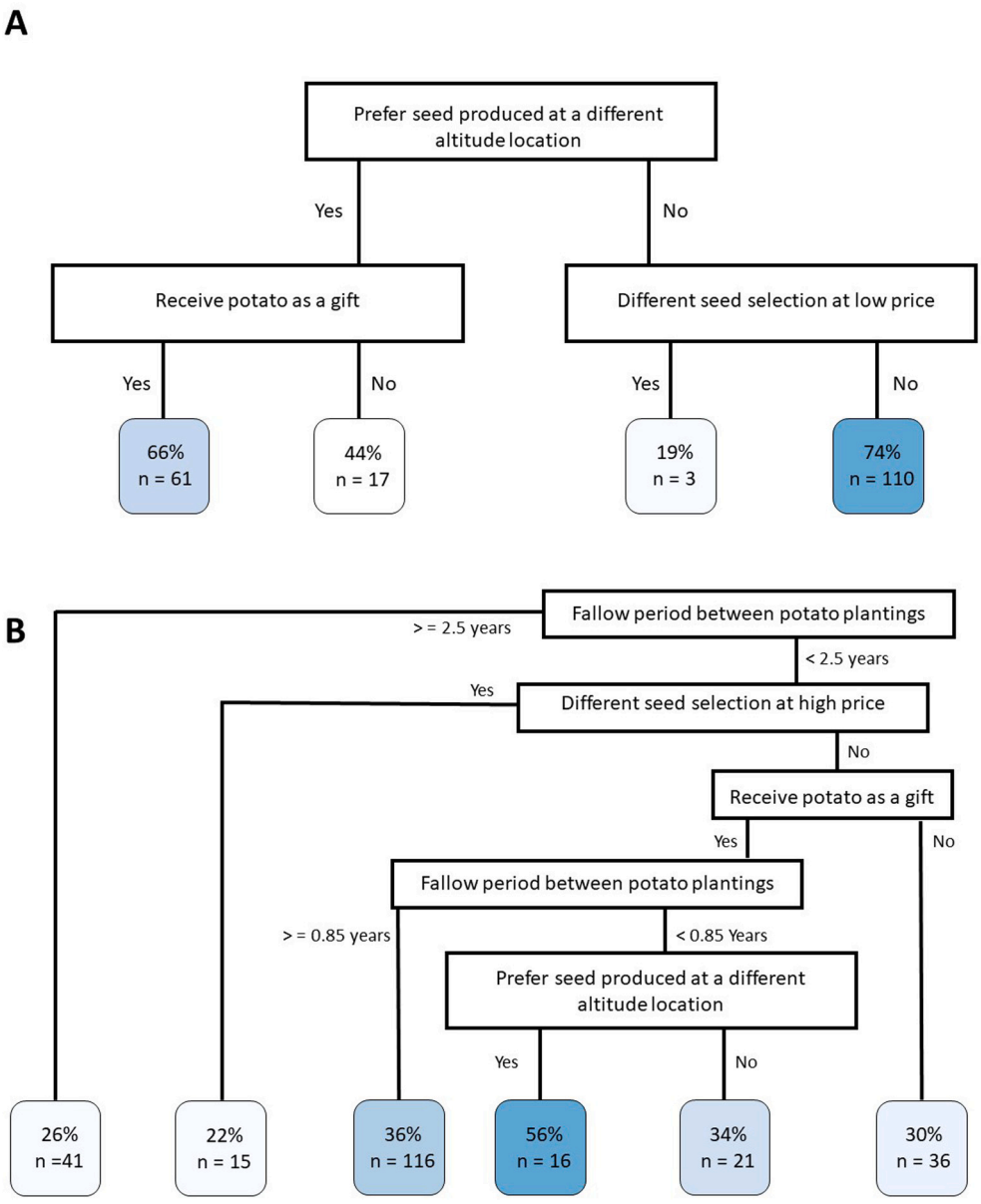

Fig. 5. Regression tree used to identify factors affecting the percentage of seed infected with viruses (A) and seed infected with other pathogens (B) in the seed lot analysis. Main factors are indicated in the squared text, and the corresponding splits are in the open text. Boxes represent the predictions of the regression tree. The boxes' first line represents the predicted percentage of seed infected with viruses (A) and other pathogens (B). The second line is the sample size. Darker colours represent higher predicted values.

varieties have a certain level of resistance to seed degeneration, particularly degeneration caused by seed-borne viruses (Forbes et al., 2020; Scurrah et al., 2009). Potentially, this perception of resistance influences farmers' decisions to continue growing these varieties since they are not presenting considerable problems with pests and diseases causing seed degeneration (Savary et al., 2012; Zeven, 1999). Under other scenarios, varieties could be replaced when farmers experienced them as susceptible. This was the case for the cassava variety Ebwanateraka, which, after being widely adopted in Uganda, was abandoned because it was susceptible to cassava mosaic disease (causal agent: Cassava Mosaic Virus) (Otim-Nape et al., 2001). Yet, it is necessary to investigate the tolerance or resistance to seed degeneration of the varieties cultivated in the Andes under different agroecological conditions. On the other hand, it could be possible that farmers experience that their seed lots do not degenerate or degenerate slowly because their yields are constrained by other major limiting factors as suggested by Navarrete et al. (2021a).

Depending on the agroecological conditions, we found that farmers replaced their seed lots of improved and native varieties after a different number of cycles of on-farm propagation (Fig. 2B). In the highlands, the seed lots of improved varieties were replaced earlier than the seed lots of native varieties (Fig. 2B). In the intervalley, seed replacement was different than in the highlands. Here, seed replacement of improved and native varieties was similar and occurred mostly between 1 and 3 years before the time of our survey (Fig. 2B). This low rate of seed replacement could be associated with the lack of farmers' concern about seed quality. A recent study revealed that only 3% of Ecuadorian farmers were concerned about the quality of their seed (Ministerio de Agricultura y Ganadería, 2019). Similarly, previous studies reported that the majority of farmers identified their seed as being of good quality (Flores et al., 2012). This implies that farmers in the Andes do not consider that low seed replacement rates could lead to seed degeneration. This finding is not new as it was already mentioned three decades ago by Crissman and Uquillas (1989). However, recent outbreaks of purple top disease (Castillo, 2020) could challenge this reality and motivate farmers to replace their seed more often.

Beyond the diversity of potato varieties and seed replacement rates, our results showed 36 on-farm seed management practices in Ecuador (Fig. 3). From these, there were several practices implemented in the same frequencies in the intervalley and in the highlands such as waiting

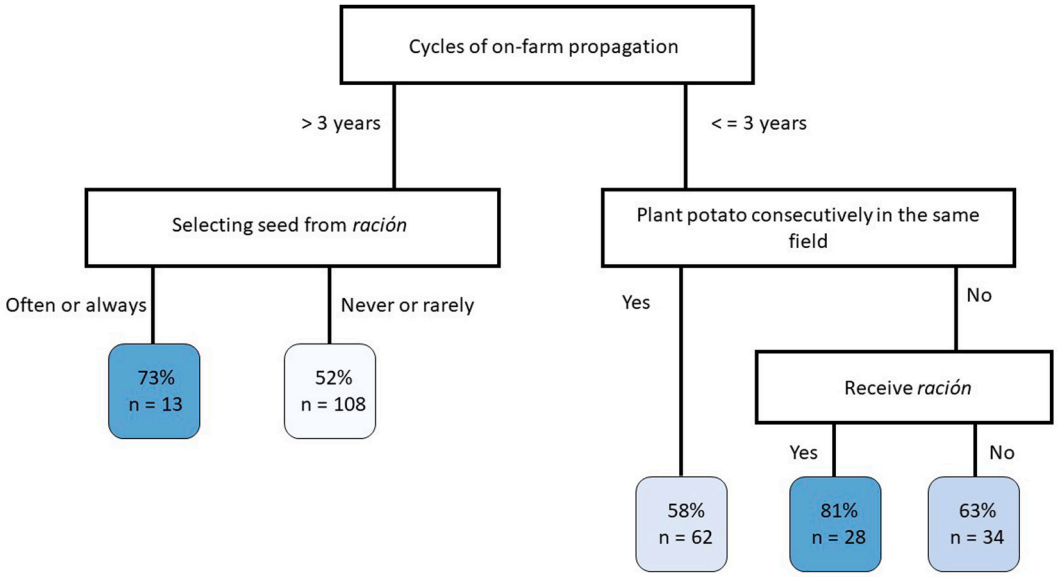

Fig. 6. Factors affecting the percentage of seed with insect damage in the farmers seed lots. Main factors are indicated in the squared text, and the corresponding splits are in the open text. Boxes represent the predictions of the regression tree. The boxes' first line represents predicted values, or the predicted percentage of seed with insect damages. The second line is the sample size. Darker colours represent higher predicted values.

for the seed to sprout or selecting the seed at harvest. We also found several seed practices associated with the agroecological conditions (Fig. 3). For example, the disinfection of the seed was more frequent among farmers in the intervalley than among those in the highlands. And, receiving *ración* was more common among the farmers in the highlands than among farmers in the intervalley. In this way, our results support the relationship between seed management practices and agroecological conditions as suggested by Almekinders et al. (1995).

4.2. *Influence of improved and native varieties and cycles of on-farm propagation on yield reduction*

Our model (Eq. (1)) showed that the type of variety and year of data collection explained most of the variation in yield (Fig. 4). Yields reported by farmers for improved varieties were in general higher than the yields reported for native varieties. On the other hand, we identified that yields between the years were distinct, and that 2010 was the year with the highest yields (Fig. 4). However, we did not find any influence of the number of cycles of on-farm propagation and agroecological conditions on yield. Our results suggest that the effect of potato seed degeneration expressed as yield reduction is not a linear process but more irregular than expected. In preceding descriptions of potato seed degeneration, Beukema and van der Zaag (1990) indicated that seed degeneration could be different between cycles of on-farm propagation. In Uganda, experiments corroborated this description, and showed that yield did not decline when farmers' seed was planted over consecutive cycles of on-farm propagation (Priegnitz et al., 2020). Unfortunately, published evidence based on experiments evaluating the yield variation associated with seed degeneration is extremely scarce in developing countries (Thomas-Sharma et al., 2016). Probably, the assumption that *yield reduction is linearly associated with seed degeneration* could discourage scientists from publishing their findings because their results are not consistent with this assumption. Confirmation bias can occur such that scientists tend to look for evidence that confirms the theory or their hypothesis (Kozlov and Zvereva, 2015; Marsh and Hanlon, 2007; Schumm, 2015). Embracing the possibility that the process of seed degeneration is not linear over the cycles of on-farm propagation could advance the understanding of this problem and its relationship with other factors across agroecological and socio-economic conditions.

Our results showed the existence of other major yield-limiting factors in the years of data collection. To name a few factors, these could have been water and nutrient availability or potato purple top disease (Castillo, 2020; Haverkort and Struik, 2015). These major limiting factors could mask (or enhance) the effect of seed degeneration on yield because they influence the presence of seed-borne pathogens in potato and the severity of infection (Adams and Stevenson, 1990; Lambert et al., 2005). Future research should focus on understanding the process of seed degeneration under different socio-ecological conditions, carefully considering the existence of major limiting factors. For this, upcoming studies could combine farmers' seed surveys and experimental plots or use the triadic approach (Van Etten et al., 2016). The information coming from these studies could motivate a discussion between farmers, extension agents, and scientists about the importance of seed, seed degeneration, and the influence of other major limiting factors on yield.

4.3. *Effect of on-farm management practices on the seed infected with viruses, other pathogens, and seed with insect damage*

In the Andes of Ecuador, a recent study demonstrated the differences between seed degeneration evaluated in experiments and farmers' fields (Navarrete et al., 2021a). The hypothesis about the differences was that on-farm seed management practices played a role in the process of degeneration in farmers' fields. Our data supports this hypothesis because we found practices affecting seed degeneration in the Ecuadorean Andes (Figs. 5 and 6). However, not all the practices contributed in the same way to degeneration. Some practices reduced seed degeneration, others accelerated it, and others increased the uncertainty because they played a double role (reducing or accelerating) depending on the cause of degeneration.

Our regression trees identified four on-farm practices reducing seed degeneration: (1) selecting seed differently when ware potato prices were either low or high in the market, (2) multiplying seed for multiple cycles of on-farm propagation, (3) planting potatoes consecutively in the same field, and (4) implementing a fallow period between potato plantings. We provide two examples to highlight how these practices reduce degeneration. The first example is selecting the seed differently at low and high ware potato prices (Fig. 5A and B). Earlier, we mentioned that it is presumed that farmers select bigger and healthier seed tubers when ware potato prices are low, and the opposite when ware potato prices are high. We found that selecting bigger and healthier

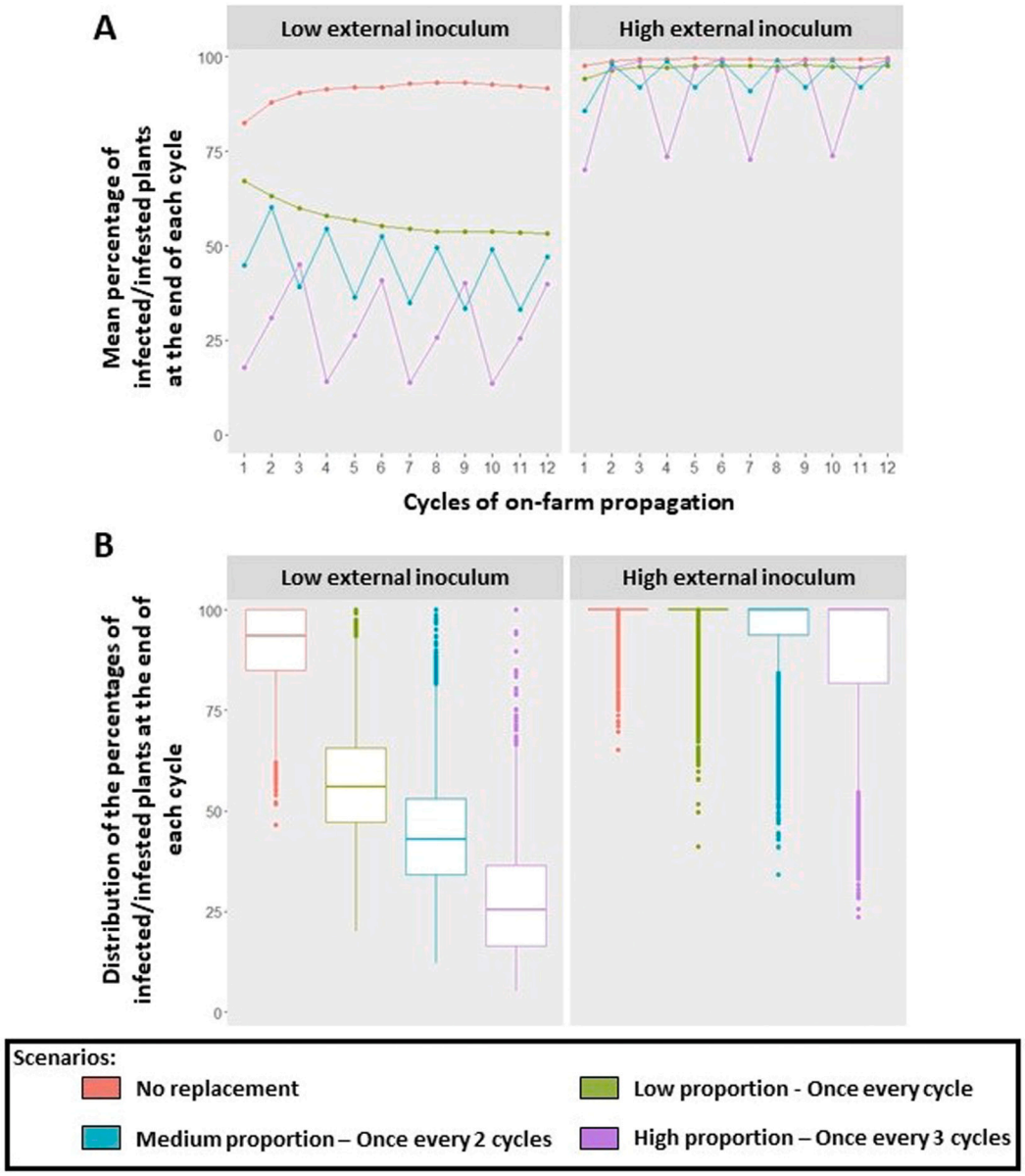

Fig. 7. Potential effect of replacing part of farmers' seed lots by healthy seed at different frequencies on the mean percentage of infected/infested plants at the end of each cycle, in scenario analyses using the seedHealth model. (A) Effect of replacing part of farmers' seed lots by healthy seed at different frequencies of replacement under low and high external inoculum conditions in each cycle of on-farm propagation. (B) Boxplots show the distribution of percentage of infected/infested plants at the end of each cycle of the scenarios evaluated. Boxplots are based on the outputs of the 12 cycles of analysis in the 400 realizations. Colours represent scenarios evaluated.

tubers decreased the percentage of seed infected with viruses and other pathogens by 55% and 11%, respectively, in comparison with not selecting the seed differently. This evidence supports the description that the quality of farmers' seed could fluctuate according to the ware potato price (Velásquez, 2006). Potentially, raising awareness about the impact of the ware potato prices on seed selection could help farmers to maintain or improve the quality of their seed. The other example is implementing a fallowing period between potato plantings. We found that farmers using fallow periods longer than 2.5 years had a lower percentage of seed infected with other pathogens (Fig. 5B). This result was expected since the reduction in the percentage of seed infected with pathogens like *Rhizoctonia solani* or nematodes due to longer fallow periods has been reported extensively (e.g., Frank and Murphy, 1977; Gilligan et al., 1996; Scholte, 1992; den Nijs, 2007).

We found different on-farm practices accelerating the process of seed degeneration in the Andes of Ecuador with smallholder farmers. These were receiving potato as a gift, receiving *ración*, and selecting seed from *ración.* We found that farmers who applied these practices had a higher percentage of seed infected with viruses, other pathogens, and with insect damages than those farmers who did not receive gifts/*ración* and select seed from *ración* (Figs. 5 and 6). This suggests that smallholder farmers are more likely to be affected by seed degeneration because they tend to select seed from gifts and *ración* (Navarrete et al., 2021b). This does not mean that technical recommendations should discourage these culturally embedded practices, but that future seed interventions need to improve farmers' capacity to select seed from these sources.

We pinpointed only one practice playing a double role (delay or accelerate) in seed degeneration depending on the cause (Fig. 5A and B): preferring the seed produced at a different altitude location as planting material. We estimated that farmers that prefered the seed produced at a different altitude location had 12% less seed infected with viruses than those farmers who did not prefer the seed produced at a different

altitude location. This finding is similar to the one observed among Peruvian farmers that plant (or purchase) their seed at high altitudes –low temperatures– to reduce the percentage of seed infected by viruses (de Haan, 2009). Our results are supported by the evidence that seed produced at high altitudes has a low probability of virus infection because there is a low incidence of insects (Gamarra et al., 2020; Kroschel et al., 2013; Salazar, 1996) and a low probability of virus transmission from infected mother plants to daughter tubers (Bertschinger et al., 2017). However, this practice had an opposite effect on the percentage of seed infected with other pathogens such as Rhizoctonia or Common scab (*Streptomyces scabies*). Farmers preferring the seed produced at a different altitude location had 12% more seed infected with other pathogens than farmers who did not prefer the seed from a different altitude location. We hypothesize that the reasons for this increase are that: (1) this preference does not interfere in the epidemiology of pathogens other than viruses, and (2) this preference increases the probability of spreading pathogens from regions where these are predominant. Further research is necessary to understand the impact of this practice in the process of degeneration caused by pathogens other than viruses.

4.4. Understanding the effects on seed degeneration of replacing only a fraction of seed with healthy seed

In the Andes, farmers could entirely or partially replace their potato seed lots (de Haan, 2009). The availability and accessibility of seed can influence farmers' choices about seed replacement, with effects on seed degeneration across seasons that need to be better understood. Using the seedHealth model we evaluated scenarios in which only a limited quantity of seed could be obtained, and this quantity was distributed as more complete replacement less frequently, or less complete replacement more frequently, where the latter may often be more practical for farmers. We evaluated these effects on the average percentage of infected/infested plants at the end of each cycle over multiple cycles of on-farm propagation. In scenario analyses, replacing low proportions of the farmers' seed lots every cycle was less effective at reducing infection/infestation over time than using the same amount of seed to replace a high proportion of the farmers' seed lots every three cycles over time (Fig. 7). Farmers may have fewer options to replace 90% of their seed lots by healthy seed at once, but even spreading this replacement across multiple cycles –as is likely more realistic– is still useful for reducing infection/infestation. Potentially, replacing a small proportion every cycle can still reduce the chances of introducing or spreading new diseases and pests into the seed lot or soil, as observed for variety mixtures (Finckh et al., 2007; Tooker and Frank, 2012; Wolfe, 1985). At the same time, partial replacement could contribute to the so called "yield compensation effect" (Salazar, 1996; Struik and Wiersema, 1999) because of the availability of healthy plants that occupy the extra space left by infected/infested plants obtaining higher yields.

The scenario analyses using seedHealth can be thought of as generating hypotheses to be validated in the field. Evaluating the performance of replacing proportions of farmers' seed lots by healthy seed over consecutive cycles of on-farm propagation under farmers' conditions will be an important step for understanding management options in this system and providing recommendations for management.

Using the seedHealth model, we identified three critical system aspects that need to be considered before recommending the partial replacement of farmers' seed lots by healthy seed. These were: the level of external inoculum, the proportion of seed replaced, and the frequency of seed replacement. Our scenario analyses illustrated how the effect of the proportions of healthy seed and the frequency of seed replacement could be influenced by low versus high levels of external inoculum (Fig. 7). These findings support previous evidence showing that the performance of improved technologies, such as new varieties or positive selection, is different depending on the agroecological conditions (Garrett et al., 2009; Nitzan et al., 2010; Priegnitz et al., 2019). This is even more important if we consider that climate change could modify the level of external inoculum in an area because of environmental impacts on the incidence and spread of pests and diseases, with potential feedbacks as higher external inoculum levels can reduce the performance of some types of management strategies (Garrett et al., 2006; Perez et al., 2010).

In the scenario analyses, the average percentage of infected/infested plants at the end of each cycle was reduced every time that some portion of the seed was replaced in the farmers' seed lot. The level of reduction was associated with the percentage of healthy seed replaced: larger reductions were observed when 90% of healthy seed was replaced than when 60% or 30% of seed was replaced (Fig. 7B), even though the overall amount of replaced seeds was the same across the twelve cycles (Fig. 7). Scenario analyses that address regional pest and disease management, such as impact network analysis (Garrett, 2021) or management performance mapping (Buddenhagen et al., 2021), could be used in follow-up studies on the effects of farmer decisions about integrated seed health strategies on disease and pest damage across larger areas. Our results also showed that the frequency of seed replacement was critical over multiple cycles of on-farm propagation. Generally, the full replacement of degenerated seed with certified seed is considered one of the most important practices to manage potato seed degeneration (Forbes et al., 2020; Gutbrod and Mosley, 2001; Thomas-Sharma et al., 2016). However, the use of certified seed is very limited in low-income countries, particularly in Ecuador and in the entire Andean region (Flores et al., 2012; Thiele, 1999). For these countries, replacing degenerated seed with small proportions of healthy seed at different frequencies could be an option to manage potato seed degeneration. This practice could also be economically attractive for farmers as it increases the profitability of potato production (Ochieng-Obura et al., 2016). These results suggest that strengthening farmers' capacity for selecting the seed that they will use for replacement could help them to have high quality seed (regardless of whether the seed comes from outside sources or not) and therefore reduce seed degeneration.

5. Conclusions

Potato varieties and on-farm seed management practices play a critical role in yield variation and seed degeneration. We found that most smallholder farmers experienced that their varieties did not degenerate or degenerated slowly. We also did not observe the expected yield decline trend for seed degeneration. We hypothesize that this is because seed degeneration -expressed as yield decline- is not a linear process but an irregular one influenced by the agroecological conditions and farmers' practices. It could also be that other major factors (e.g., water deficiency) are masking seed degeneration and thereby hampering the identification of the expected yield decline trend (Navarrete et al., 2021a). In light of this new evidence, it becomes critical to understand how farmers experience seed degeneration. Also, we identified an assemblage of on-farm seed management practices implemented in the Andes of Ecuador. There were practices implemented commonly by farmers in the province of Cotopaxi, but other practices were implemented depending on the agroecological conditions. Seed interventions should consider the relationship between practices and agroecological conditions to identify regions where capacity building is necessary. Our research showed that on-farm management practices play a critical role in seed degeneration. Yet, this role is barely acknowledged in the literature. We found that several practices reduced or accelerated seed degeneration, and other ones played either role depending on the cause of degeneration. Moreover, we found that replacing a part of the farmers' seed lot by healthy seed is a potential practice to manage seed degeneration in countries where full replacement with certified seed is not an option. We urge scientists, practitioners, farmers, and policy makers to identify opportunities for improving on-farm practices that have the potential to manage degeneration efficiently.

Authors' contribution

I. Navarrete designed and performed the research, collected and analysed the data, and led the writing of the manuscript. V. López, R. Borja, P. Oyarzún supported the data collection and assisted with the interpretation of the information and the writing of the manuscript. K.A. Garrett and Y. Xing assisted with the implementation of the seedHealth model and the writing of the manuscript. C.J.M. Almekinders, J.L. Andrade-Piedra, and P.C. Struik assisted with the design, analysis, and interpretation of the information and assisted with the writing of the manuscript. All authors reviewed the manuscript critically and approved the submitted version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.agsy.2022.103387.

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