



Agroecological settings and seed recycling account only partially for potato seed degeneration in Ecuador

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Abstract

Potato production in low-income countries is threatened by seed degeneration, i.e., the accumulation of seed-borne diseases and pests in potato seed tubers when these are vegetatively propagated over consecutive cycles, leading to a reduction in seed quality and yielding ability. Agroecological settings and seed recycling (on-farm propagation over consecutive cycles) determine the process of seed degeneration. However, it is poorly understood how these factors affect this process. Therefore, to reduce this knowledge gap, we analysed two datasets collected in Ecuador, one from a multi-annual field experiment and one from a farmers' seed study. The experiment, carried out from 2013 to 2016, aimed to assess seed degeneration at agroecological settings present in three different altitudes. The farmers' seed study, in which 260 farmers were surveyed in 2018, aimed to understand potato seed degeneration in farmers' fields under diverse agroecological settings. Our results of the multi-annual field experiment showed that agroecological settings have a heterogeneous influence on the presence of seed-borne diseases and pests. We also found that both the agroecological settings at the three altitudes and the number of on-farm propagation cycles affected the rates at which seed-borne diseases and pests on the seeds increased and yield decreased. However, the farmers' seed study challenged these results by indicating that this was not clear on farms. Combining these results, this article shows that agroecological settings and seed recycling only partially explain the process of seed degeneration. This suggests that more research about seed degeneration needs to also take place under farmers' conditions to fully understand the complex of potato performance factors. We expect that such research will support the design of improved seed interventions, while simultaneously it may generate discussion about when potato seed degeneration plays an important role in productivity.

Keywords Farmers' fields · *Solanum tuberosum* · Seed replacement · Seed systems · Yield-limiting factors

1 Introduction

Potato (*Solanum tuberosum*) seed degeneration is defined as the build-up of pests and pathogens in seed tubers (hereafter seed; Fig. 1) when farmers propagate their seed vegetatively over consecutive cycles of on-farm multiplication, leading to a reduction in seed quality and presumably yield (Struik and Wiersema 1999; Whitehead 1930; Fig. 2). This degeneration process starts when healthy mother plants or their offspring become infected/infested either in the field, in the storage, or by already infected seed tubers. Once mother plants are infected/infested, pests and pathogens spread to the daughter tubers. This spreading can depend on the pests or pathogens infecting/infesting the mother plant and the interactions among them (Grupa et al. 2018), the level of infection or infestation, the potato variety's resistance,

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Fig. 1 Farmers' potato seed stored for the next planting season. Photograph taken by I. Navarrete/WUR-CIP.

agroecological settings, and the moment of infection/infestation affecting pathogen spreading through restrictions associated with plant maturity (Bertschinger et al. 2017; Dupuis 2017). Only a proportion of the daughter seeds might become infected/infested to such an extent that they develop

into carriers and transmitters themselves (Bertschinger et al. 2017) (Fig. 2).

Estimating the proportion of infected/infested seed tubers and the level of infection/infestation of the seed tubers (e.g., inoculum density or virus titre) is necessary to directly determine the level of seed degeneration of a seed lot: a high percentage of infected/infested seeds with high levels of infection/infestation indicates high degeneration (Fig. 2). The direct outcome is presumed to be the progressive decline in the quality of the seed lot over on-farm propagation cycles as pests and pathogens accumulate on or in the seed tubers (Struik and Wiersema 1999; Thomas-Sharma et al. 2016). We define seed quality as the genetic, physiological, physical, and health characteristics that affect the seed tubers' ability to produce plants that deliver high yields of daughter tubers. A decline in yield with seed degeneration is indirectly expected, as yield is associated with seed quality (Struik and Wiersema 1999; Thomas-Sharma et al. 2017) (Fig. 2). However, yield decline at low levels of seed degeneration could be compensated by enhanced yield from neighbouring plants (compensation effect) (Salazar 1996; Struik and Wiersema 1999). Yield decline associated with seed degeneration could also be compensated by the effects of cross-protection, a phenomenon in which a pre-existing pathogen infection prevents secondary infections or more

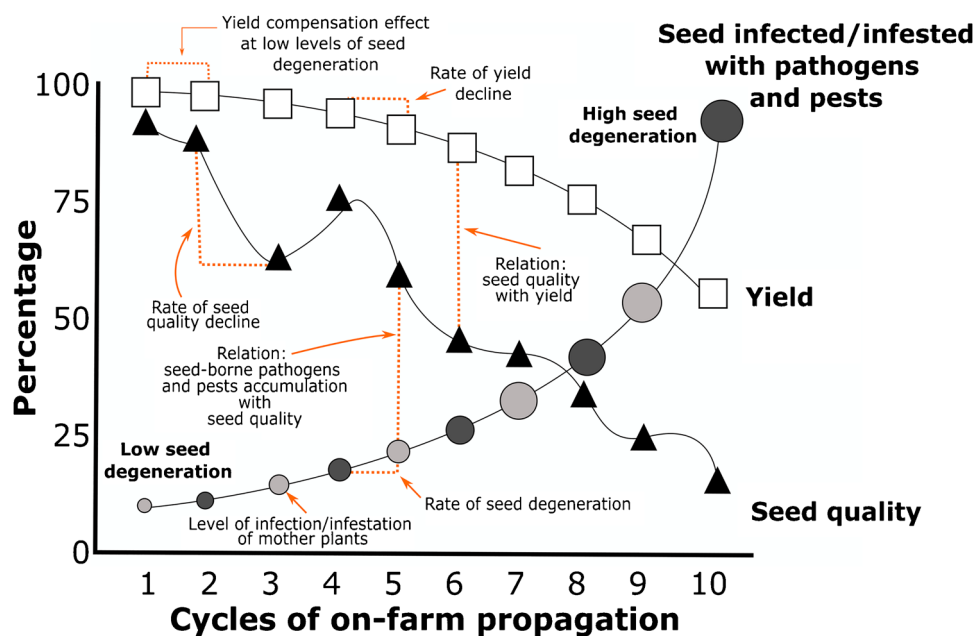


Fig. 2 Theoretical process of potato seed degeneration and critical relationships. This figure was created based on the descriptions presented by Beukema and van der Zaag (1990), Salazar (1996), Struik and Wiersema (1999), and Thomas-Sharma et al. (2017). Critical relationships for the process of seed degeneration are in orange. The curve of “Seed infected/infested with pathogens and pests” contains

circles with different shades of grey and sizes. Shades of grey represent levels of infection/infestation of mother plants as these levels could change in each growing season. Lighter shades indicate low levels of infection/infestation while darker shades represent high levels of infection/infestation. The size of the circles represents the proportion of infected/infested seed in the lot.

severe disease caused by another pathogen strain (Ponz and Bruening 1986) (Fig. 2).

As mentioned previously, seed degeneration rates could change with variations in agroecological settings (e.g., temperature or crop diversity) as these determine: (1) the presence and rate of development of seed-borne pests and pathogens, (2) the vector pressure, and (3) the presence of resistant potato varieties (Thomas-Sharma et al. 2017). Drawing from examples on viruses, scientific reports have suggested that agroecological conditions could either facilitate the accumulation of viruses like in the Cañete Valley in Peru (Bertschinger 1992) or limit this accumulation as in the case of Island Grande del Tierra del Fuego in Argentina (Caldiz et al. 1999), but there is a poor understanding of when or how agroecological settings facilitate or limit seed degeneration depending on, for example, interactions among pest or pathogen populations and specific host plant characteristics. Nevertheless, it is assumed that warm areas often facilitate seed degeneration, whereas cold areas slow seed degeneration (Thomas-Sharma et al. 2016). This assumption about warm and cold areas applies when pests (e.g., aphids) and pathogens (e.g., viruses) are affected by temperature, but ignores other factors. *Rhizoctonia solani* or nematodes, for example, cause seed degeneration under high-humidity or high-cropping-intensity conditions. The lack of understanding of the impact of agroecological settings on the process of seed degeneration could be the foundation of these general assumptions and may mislead the design of interventions to improve seed quality.

Although seed degeneration presumably leads to a gradual decline in yield across on-farm propagation cycles (Fig. 2), there is little empirical evidence confirming this assumption (Thomas-Sharma et al. 2016). Examples of the impact on productivity caused by diseases leading to seed degeneration can be found for Potato Virus Y (PVY) and Potato Leaf Roll Virus (PLRV), which can cause reductions in yield between 50 and 90% (Rahman et al. 2010). Another well-documented example is bacterial wilt (causal agent, *Ralstonia solanacearum*), which can cause total yield losses (Uwamahoro et al. 2018). However, these studies only show the impact of different degrees of pests and disease incidences/severity on yield and do not show the assumed progressive decline in yield resulting from the continuous propagation of seed. According to Thomas-Sharma et al. (2016), another way of estimating yield losses associated with seed degeneration is by comparing the productivity obtained in experiments evaluating seed management strategies. In Kenya, it was estimated that the use of degenerated seed reduced the yield on average by 34% when compared with seed coming from positive selection (Gildemacher et al. 2011). Either using experiments or comparing seed sources, the estimated yield

losses may be conservative because of the compensation effect (Salazar 1996; Struik and Wiersema 1999). Nevertheless, it is critical to assess yield losses associated with seed degeneration to identify the best strategies for seed system interventions.

The Andes is one of the regions in the world where it is unclear how the large variation in agroecological settings affects the accumulation of pathogens and pests on/in seed. However, some general observations about the presence of these pathogens and pests are deemed to be valid. In the lowlands of the Andes, there is a high abundance of insect vectors (e.g. *Macrosiphum euphorbiae*), viruses transmitted by insects, and high virus secondary infection rates (i.e. proportion of daughter tubers infected by the mother plant; Bertschinger 1992; Bertschinger et al. 2017; Luque et al. 1991). In the highlands, insect vectors are less abundant. For instance, Fankhauser (2000) found only up to 20 aphids/trap/month in potato fields planted at altitudes above 3080 m above sea level (m asl). The presence of important seed-borne viruses like PVY and PLRV is also very limited (Fankhauser 2000; Kreuze et al. 2020; Kromann et al. 2014; Navarrete et al. 2017; Scurrah et al. 2009). In contrast, other important seed-borne pests and diseases are present in the highlands, such as black scurf (*Rhizoctonia solani*), the Andean weevil (*Premnotrypes vorax*), or the potato tuber moth complex (*Tecia solanivora*, *Symmetrischema tango-lia*s, and *Phthorimaea operculella*, hereafter tuber moth) (Fankhauser 2000; Navarrete et al. 2017). Hence, understanding seed degeneration in the Andes requires consideration of the local agroecological settings.

Observations in the Andes suggest that the rate of seed degeneration is variable in farmers' seed lots. Farmers' management might (or might not) reduce the quality of the seed. In the Andes, farmers select preferably small (egg-sized) tubers from previous harvests as seed for the next season and call them 'their own seed' (Crissman and Uquillas 1989; Kromann et al. 2016). As this occurs over consecutive cycles, this practice could enable the accumulation of pests and diseases on the seed and reduce seed quality (Fig. 2). Replacing degenerated seed with healthy seed is one practice to manage seed degeneration (Thomas-Sharma et al. 2016). However, the only reasons motivating farmers to replace their entire seed lot are when (a) extraordinary weather events like frost, hail, or drought occur; (b) they want to access new cultivars; or (c) their seed 'gets tired' (referring to degenerated seed) (de Haan 2009; Thiele 1999). Farmers could include potatoes received as gifts or *ración*—in-kind payment in the form of tubers—or potatoes coming from the market, relatives, or friends (Crissman and Uquillas 1989; de Haan 2009). These practices create uncertainty about farmers' seed quality and how that affects their yield, thus making it more difficult to recommend practices to manage seed degeneration. Moreover, farmers' current storage techniques, such as the use of

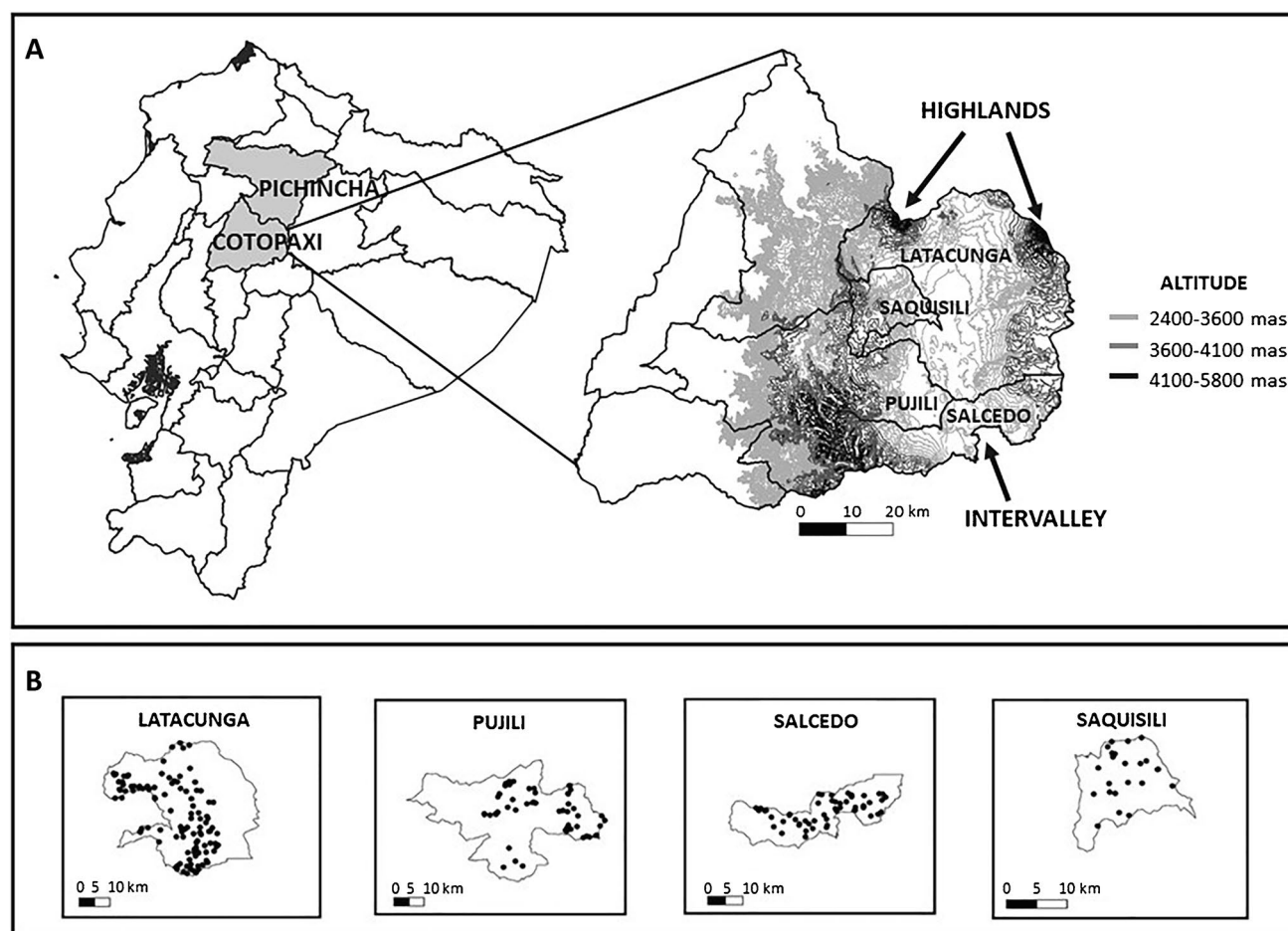


Fig. 3 Location of the studies performed in Ecuador. **A** On the left, the provinces of Pichincha (study 1) and Cotopaxi (study 2) in Ecuador (in grey) and, on the right, Cotopaxi's administrative map showing the variation in altitude and the location of highlands and

the intervalley. **B** Main potato-producing cantons in Cotopaxi. Dots represent the places where the farmers' seed study (study 2) was performed.

straw cylinders or net bags, could facilitate an increase in seed-borne insects that cause seed degeneration (de Haan and Thiele 2003; Thomas-Sharma et al. 2016).

All these uncertainties about the state of seed degeneration in farmers' seed lots lead to the following question: What does seed degeneration look like in the Andes? This question is very broad, but this paper aims to deepen our understanding about the influence of Andean agroecological settings and seed recycling (continuous on-farm propagation) on the process of potato seed degeneration, expressed as the percentage of infected/infested tubers and yield. We answer this research question using data collected from a multi-annual field experiment and a farmers' seed study. We expect that our results will trigger a discussion about how to strengthen seed systems in the Andes and in other countries where seed degeneration remains a problem.

2 Methodology

We used data from two studies conducted in Ecuador to understand the effect of agroecological settings and seed recycling on potato seed degeneration. In the first study, we performed a multi-annual field experiment in Pichincha province (Fig. 3A) to evaluate potato seed degeneration at three different altitudes, as proxies for different ecological settings. In the second study, we performed a farmers' seed study by surveying farmers and analysing their seeds to understand potato seed degeneration under different agroecological settings in four cantons in Cotopaxi province (Fig. 3A, B).

2.1 Geographic, climatic, and productivity conditions in the study areas

The mountain regions of the provinces of Pichincha and Cotopaxi in Ecuador are characterized by an intervalley and two highland areas (the *Oriental* (eastern) and *Occidental* (western) ranges) (Fig. 3A) (Andrade et al. 2002; Lips 1998; Moreno et al. 2018). Farmers cultivate potato in the intervalley and the highland slopes, between 2400 m asl and 3800 m asl (Andrade et al. 2002). These provinces together account for 15% of national potato production in Ecuador (Sistema de Información Pública Agropecuaria 2020).

The mean temperature in the experimental plots planted in Pichincha (study 1) ranged from 10.0 to 15.1 °C, and the mean accumulated rainfall per growing period ranged from 571 to 796 mm (Table 1). In Pichincha, 91% of the farmers use their own seed, and their yields reach on average 25 t ha⁻¹ (Ministerio de Agricultura y Ganadería 2019).

In Cotopaxi province (where study 2 took place), the major potato production areas are the cantons of Latacunga, Pujilí, Salcedo, and Saquisilí (Fig. 3B). The temperature in the highlands is on average 8.9 °C, whereas in the intervalley, the temperature is higher (12.5 °C) (Table 1). Furthermore, the highlands experience more rainfall per year (931 mm) than the intervalley (637 mm) (Table 1). In Cotopaxi, 94% of the farmers reported using their own seed, and their yields reached on average 11 t ha⁻¹ (Table 1) (Ministerio de Agricultura y Ganadería 2019). In this province, frost is a serious problem that occurs in January, February, May, August, October, and November (Hibon et al. 1995).

2.2 Study 1: Multi-annual field experiment

2.2.1 Description of experimental plots and data acquisition

From November 2013 to February 2016, three cycles of potato crops were grown in experimental plots planted at three altitudes in Pichincha within and near the research station of the International Potato Center, Quito (CIP-Quito). The plots (area = 49 m² per plot) were planted with approximately 164 certified seed tubers (levels of pests and diseases in/on the seed were below thresholds established in the national seed regulation) of the Super chola variety in the first cycle. We selected this variety because it is the most common in the country. In the following cycles, the harvested seed from the previous cycle was used as planting material. From the first year, one plot was planted in each of the following three altitudes: below 3000 m asl, at approximately 3000 m asl (hereafter 3000 m asl), and above 3000 m asl (Table 1). All experimental plots were managed by members of the research team. In the same experiments, also the INIAP-Fripapa variety and several on-farm seed

Table 1 Summary of climate data and agronomic practices in the provinces and experimental areas studied. Sources: Fick and Hijmans (2017), Kromann et al. (2017), Instituto Nacional de Estadística y Censos (2019), Ministerio de Agricultura y Ganadería (2019). *Accumulated rainfall in the multi-annual field experiment was measured during the growing period using rain gauges; in the farmers' seed study, it was estimated from WorldClim2.

	Pichincha (Study 1)	Cotopaxi (Study 2)
Mean elevation (m asl)		
Study 1. Multi-annual field experiment		
Above 3000 m asl	3507	
At about 3000 m asl	3050	
Below 3000 m asl	2649	
Study 2. Farmers' seed study		
Highlands		3497
Intervalley		2954
Mean temperature (°C)		
Study 1. Multi-annual field experiment		
Above 3000 masl	10	
At about 3000 masl	12	
Below 3000 masl	15	
Study 2. Farmers' seed study		
Highlands		9
Intervalley		13
Mean accumulated rainfall		
Study 1. Multi-annual field experiment (mm growing period ⁻¹)*		
Above 3000 masl	796	
At about 3000 masl	571	
Below 3000 masl	576	
Study 2. Farmers' seed study (mm year ⁻¹)*		
Highlands		931
Intervalley		637
Farmers planting their own seed (%)	91	94
Mean potato field size (ha)	2.1	0.5
Potato yield (t ha ⁻¹)	25	11

management practices were evaluated, but these data were not used in the current study.

Total yield per plant and the incidences of bacterial, fungal, and viral diseases and insect damage were evaluated in each cycle. Total yield per plant (in kg) was measured on average on 73 plants per plot at harvest with each plant having neighbouring plants. Total yield per plant was converted into yield per hectare in two steps. In the first step, we estimated the yield per plot by adding up the productivity of the evaluated plants at harvest (in kg) and multiplying this by the number of planted seed tubers ($n = 164$) in the plot. Then, we divided this value by the number of evaluated plants in the plot. In the second step, the estimated yield per plot was converted into tons per hectare using for this the productivity and the size of the experimental plot. From each

of these plants evaluated per plot, four tubers (considered the sample) were randomly selected to visually assess the presence of bacterial, fungal, and viral diseases and insect damage (James 1971). Damage caused by both the Andean weevil and the tuber moth was assigned to the same category because both pests produce similar galleries on the tuber. DAS-ELISA (CIP 2007) was used per seed sample to evaluate the incidence of Potato Virus X (PVX), Potato Virus S (PVS), Andean Potato Latent Virus (APLV), Andean Potato Mosaic Virus (APMoV), Potato Virus Y (PVY), and Potato Leaf Roll Virus (PLRV). Using this information, we estimated the percentage of seed samples infected with viruses, insect damage, and *other pathogens* per plot. We used the label *other pathogens* in the next sections of this manuscript to group the pathogens that are different from viruses such as fungi (e.g., *R. solani*) or bacteria (e.g., common scab (*Streptomyces scabies*)). The raw data from these experiments can be found in Kromann et al. (2017).

2.2.2 Multi-annual field experiment statistical analysis

The statistical analysis of the multi-annual field experiment focused on: (1) estimating the percentage of seed samples infected with diseases or with insect damage in the agroecological settings present at the altitudes at which the experiments were planted, (2) estimating the relation between the percentage of seed samples infected/infested with pathogens and pests and the number of cycles of on-farm propagation in the agroecological settings present at the altitudes at which the experiments were planted, and (3) identifying the relation between yield and the number of cycles of on-farm propagation in the agroecological settings present at the altitudes at which the experiments were planted.

The percentage of seed samples infected/infested with seed-borne pathogens and pests at the different altitudes was estimated using descriptive statistics. We also evaluated if the percentages of seed samples infected/infested with pathogens and pests were associated with the agroecological settings present at the altitudes at which the experiments were planted using chi-square tests. Moreover, we performed beta regressions (Douma and Weedon 2019) to understand the relation between the percentage of seed samples infected with viruses (P_v), seed samples infected with other pathogens (P_o), and seed samples with insect damage (P_i) with the number of cycles of on-farm propagation ($Cycle_j$) and the different altitudes ($Altitude_k$; Eq. 1). Pairwise comparisons, using Tukey tests, were performed to detect statistical differences between the cycles of on-farm propagation and between the agroecological settings at the altitudes at which the experiments were planted.

$$P_{v,o,i} \sim Cycle_j + Altitude_k + Cycle * Altitude_l + \epsilon_{jkl} \quad (1)$$

Equation 1. Generic regression equation to estimate the percentage of seed samples infected with viruses, seed samples infected with other pathogens, and seed samples with insect damage as a function of the number of propagation cycles and the settings present at the altitudes at which experimental plots were planted. $Cycle_j$ represents the number of cycles of on-farm propagation in the experiment. $Altitude_k$ represents the agroecological settings present at the altitudes at which experiments were planted. $Cycle * Altitude_l$ represents the combination of the different levels of both factors. ϵ_{jkl} represents the error of the formula.

A hierarchical regression (Eq. 2) was applied to understand yield variability caused by the number of propagation cycles ($Cycle_j$; fixed effect) and by the agroecological settings present at the different altitudes at which the experiments were conducted ($Altitude_k$; random effect). We used the lmer function in the lme4 R package (Bates et al. 2015). After this, we applied a Tukey test to identify the differences between the levels of the significant factors. We did not perform a regression between yield and the percentages of seed samples infected with virus, infected with other pathogens, or with insect damage because of the low number of observations.

$$Yield \sim Cycle_j + Altitude_k + \epsilon_{jk} \quad (2)$$

Equation 2. Regression to estimate the variation in yield associated with the number of propagation cycles and the agroecological settings present at the altitude at which the experimental plots were planted. $Cycle_j$ represents the number of cycles of propagation in the experiment. $Altitude_k$ represents the different agroecological settings at the altitudes at which experiments were planted. ϵ_{jk} represents the error of the formula.

2.3 Study 2: Farmers' seed study

2.3.1 Description of farmers' seed study

Between September and October 2018 (beginning of the main planting season), we surveyed 260 households in four cantons in Cotopaxi province (Fig. 3B). We identified the places for the surveys by overlapping the altitude map of the province of Cotopaxi with a map containing 260 grid squares. We surveyed one randomly selected household approximately at the centre of each grid square. In each household, female or male farmers were asked about their crop and potato varieties and the number of on-farm propagation cycles (in years) of their seed since they obtained each potato variety. We grouped the answers of the number of on-farm propagation cycles in four categories as farmers in some cases provided periods of time. These four categories were (1) less than 1 year (includes varieties obtained

up to 1 year and represented by “< 1”; $n = 64$ farmers), (2) between 1 and 3 years (includes varieties obtained up to 3 years and represented by “1–3”; $n = 68$ farmers), (3) more than 3 years up to and including 10 years (represented by “3–10”; $n = 79$ farmers), and more than 10 years (represented by “> 10”; $n = 49$ farmers). In case farmers had more than one variety, the category of the number of on-farm propagations assigned represents the median of the number of on-farm propagation cycles. To estimate the yield of each variety, we first asked farmers about the number of 45.45-kg bags (100 lbs, common potato bag size in Ecuador) planted and the number of 45.45-kg bags harvested in the previous cycle. Then, we calculated a multiplication ratio dividing the number of bags harvested by the number of bags planted. We estimated yield using this multiplication ratio because farmers often plant more than one seed per planting hole depending on the seed size (first, second, third, and fifth author, personal observations). Another reason for doing so was because this multiplication ratio is more meaningful for farmers than tons per hectare. We excluded and did not estimate the yield of varieties with incomplete information.

To evaluate seed quality, farmers were invited to provide a sample of seed tubers (median = 10 tubers per sample) belonging to one variety. Some farmers provided more than one sample. These tubers were then transported to CIP-Quito for a seed quality analysis. Upon arrival, the incidences of bacterial and fungal diseases and insect damage on the tubers (number of seed lots evaluated = 245) were assessed visually (James, 1971). We grouped together the galleries produced by the Andean weevil and the tuber moth as we had done previously for the experimental plots. Then, all the sprouted tubers from the sample were planted in 5-L pots in the CIP-Quito screenhouses. Leaf samples were taken when plantlets were 15 to 20 cm tall. After this, sap was extracted and used to test for PVX, PVS, PVY, PLRV, APLV, and APMoV using DAS-ELISA (CIP 2007) in 191 seed lots. This number was lower than the original number of samples taken as some tubers did not emerge because of high physiological age or insect damage. With this information, we estimated the percentage of seed tubers infected with virus, infected with other pathogens, and with insect damage, per farmer's seed lot.

Data from the farmers' seed study can be found in Navarrete et al. (2018, 2019).

2.3.2 Farmers' seed study statistical analysis

Before analysing the survey data collected in our farmers' seed study, we characterized and classified the agroecological settings of the individual farmers in Cotopaxi province. Climate and soil data were obtained using the information available in WorldClim2 (30 s resolution, Fick and Hijmans 2017), the Global Soil Organic Carbon Map (v1.5.0, FAO 2018), and the geographic locations of the farmers' surveys

(Fig. 3). From WorldClim2, we collected several climate variables using the geographic locations of the farmers' surveys: (1) monthly minimum temperature ($^{\circ}\text{C}$), (2) monthly maximum temperature ($^{\circ}\text{C}$), (3) monthly mean temperature ($^{\circ}\text{C}$), (4) accumulated rainfall (mm year^{-1}), (5) solar radiation ($\text{kJ m}^{-2} \text{day}^{-1}$), (6) wind speed (m s^{-1}), and (7) water vapour pressure (kPa). From the Global Soil Organic Carbon Map, we obtained the estimated amount of accumulated soil organic carbon (t ha^{-1}) from each place surveyed. We complemented the dataset with agronomic data reported by farmers in the survey: the number of crops grown by the farmer and the number of potato varieties. Then, we combined a principal component analysis (keeping three dimensions, cumulative percentage of variance = 73%) with a cluster analysis. This resulted in the identification of only two agroecological settings: the intervalley and the highlands (Table 1). Next, we mapped each survey to one of the agroecological settings.

The association of these agroecological settings with the incidence of seed-borne pathogens was analysed using descriptive statistics and t tests. We performed binomial mixed regressions using Eq. 1 to estimate the effects of agroecological settings and the number of on-farm propagation cycles on the accumulation of the percentage of seed tubers infected with viruses, infected with other pathogens, and with insect damage. The categories of the number of on-farm propagation cycles were considered a fixed effect, and the agroecological settings were random effects. The regression was performed using the glmer function in the lme4 R package. We also estimated the influence of the agroecological settings on the differences in yield associated with seed degeneration. We performed a hierarchical regression using Eq. 3. To do this, we initially included all the variables in the regression including their interactions. However, as the outputs of the model did not show any significant statistical interaction, we simplified the model to only consider single effects as shown in Eq. 3. All variables were kept in the model to identify the influence of fixed and random effects. Hence, in this regression, the response variable was yield (number of bags harvested/the number of bags planted), and the fixed effects were the percentage of seed infected with virus (P_v), the percentage of seed infected with other pathogens (P_o), the percentage of seed with insect damage (P_i), and the categories of the number of on-farm propagation cycles (Cycle_j). Agroecological settings ($\text{Agroecological setting}_k$) were considered random effects.

$$\text{Yield} \sim P_v + P_i + P_o + \text{Cycle}_j + \text{Agroecological setting}_k + \epsilon_{vijk} \quad (3)$$

Equation 3. Hierarchical regression to account for the differences in yield associated with the percentage of seed infected with viruses (P_v), infected with other pathogens (P_o), with insect damage (P_i), and the number of on-farm propagation cycles in different agroecological settings. Cycle_j represents the categories of the number of on-farm propagation cycles

since farmers obtained a potato variety. *Agroecological setting_k* represents the two agroecological settings identified in the province of Cotopaxi: the intervalley and the highlands. \mathcal{E}_{viojk} represents the error of the formula.

3 Results

The results for the incidence of diseases/insect damage and seed degeneration are presented firstly for the multi-annual field experiment and then for the farmers' seed study.

3.1 Study 1: Multi-annual field experiment

3.1.1 Incidence of bacterial, fungal, and viral diseases and insect damage

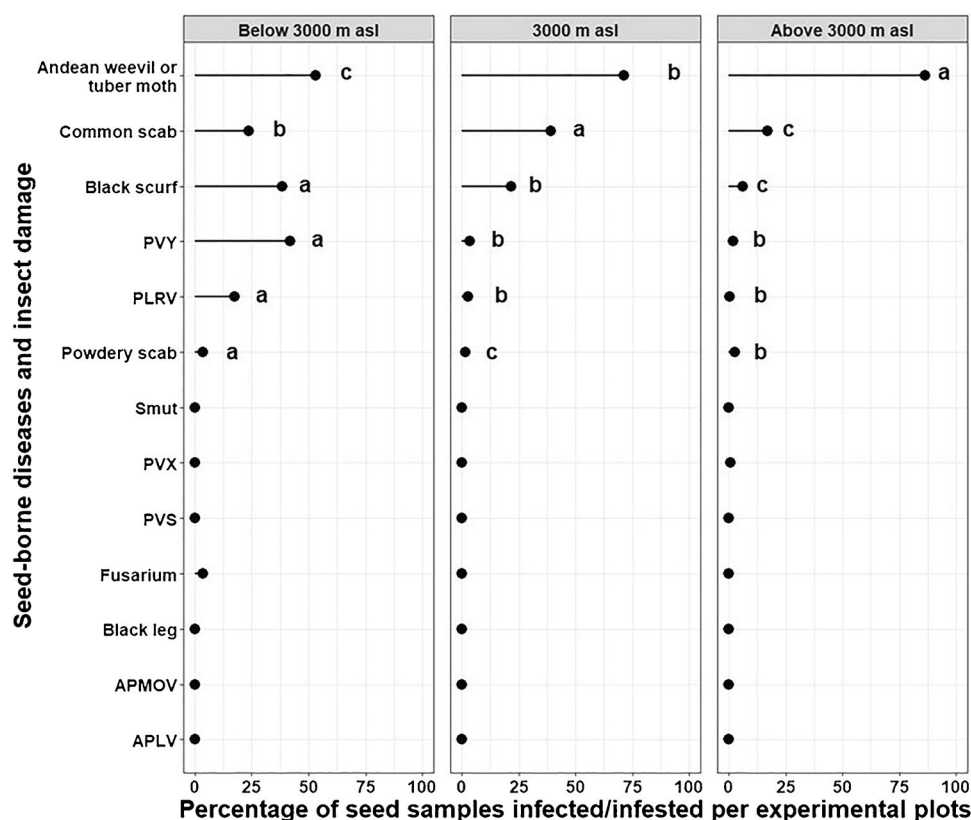
Analysing the patterns in Fig. 4, we observed that the Andean weevil or the tuber moth, common scab, black scurf (sclerotia of *Rhizoctonia solani*), and PVY were predominant in the seed samples, and their incidence differed between agroecological settings present at the altitudes at which experimental plots were planted ($p < 0.05$).

In plots planted below 3000 m asl, damage attributed to the Andean weevil or the tuber moth was found on average on 53.1% of the seed samples assessed during the three

on-farm propagation cycles (Fig. 4). This incidence was significantly lower than the incidences found in plots planted at and above 3000 m asl during the three on-farm propagation cycles ($p < 0.05$). We also frequently identified seed samples infected with PVY (mean_{of on-farm propagation cycles} = 41.9%) and black scurf (mean_{of on-farm propagation cycles} = 38.4%) in plots planted below 3000 m asl (Fig. 4). For the case of PVY, the incidence in plots planted below 3000 m asl was significantly higher ($p < 0.05$) than in plots located at and above 3000 m asl (mean_{of on-farm propagation cycles} = 3.30% and 1.84%, respectively). For the case of black scurf, the incidence in agroecological setting present in plots planted below 3000 m asl was significantly higher ($p < 0.05$) than in the other agroecological settings (mean_{of on-farm propagation cycles} at 3000 m asl = 21.7%; mean_{of on-farm propagation cycles} above 3000 m asl = 6.0%).

In the agroecological settings present in plots planted at and above 3000 m asl, the seed samples frequently showed damage of the Andean weevil or the tuber moth with mean incidences of 71.1% and 86.5%, respectively, during the three on-farm propagation cycles (Fig. 4). The incidence of the Andean weevil or the tuber moth was significantly lower at 3000 m asl than above 3000 m asl ($p < 0.05$). We found common scab at 3000 m asl with a mean incidence of 39.2% and above 3000 m asl with a mean incidence of 16.9% during the three on-farm propagation cycles. The presence of black scurf was also found at and above 3000 m asl with mean incidences of 21.7%

Fig. 4 Mean percentage of seed samples infected with different diseases and with insect damage in experimental plots at different altitudes. Data are means of three on-farm propagation cycles per altitude. The number of assessed samples during the three on-farm propagation cycles was 188 in the experimental plots planted below 3000 m asl, and 233 in the plots planted at and above 3000 m asl. Letters (a–c) indicate significant differences at the 0.05 level between agroecological settings. Absence of letters indicates no significant difference.



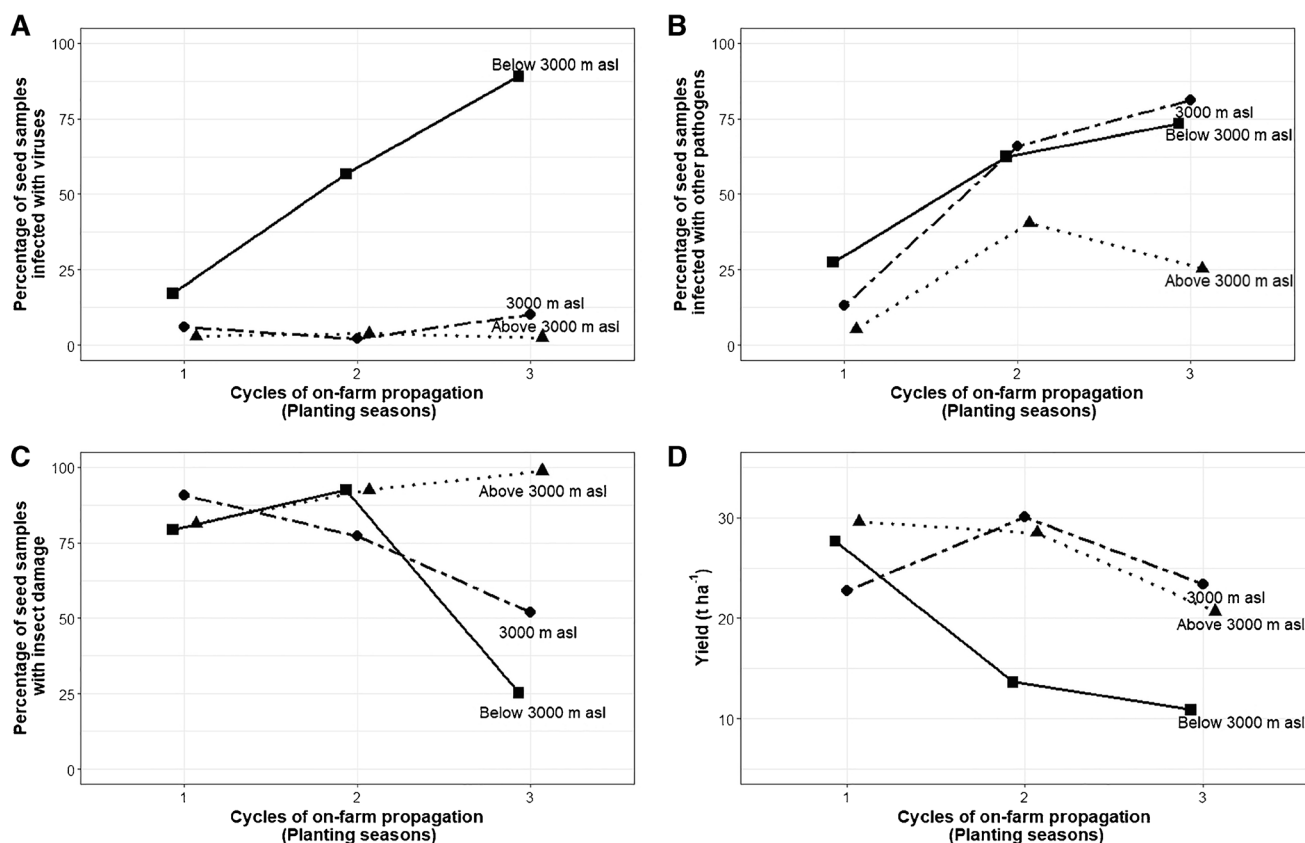


Fig. 5 Percentage of seed samples infected with seed-borne diseases and insect damage and yield per hectare over consecutive propagation cycles in experimental plots planted at different altitudes. **A** Percent-

age of seed samples infected with viruses. **B** Percentage of seed samples infected with pathogens other than viruses. **C** Percentage of seed samples with insect damage. **D** Yield (t ha⁻¹).

and 6.0%, respectively, during the three on-farm propagation cycles (Fig. 4). This presence was significantly higher in plots planted at 3000 m asl than in plots planted above 3000 m asl ($p < 0.05$). Several other pathogens were occasionally but rarely identified, such as APMoV or smut (*Tecaphora solani*). We did not find other phytosanitary problems such as bacterial wilt.

3.1.2 Seed degeneration observed in the multi-annual field experiment

In this section, we describe seed degeneration as the percentage of seed samples infected with viruses, infected with other pathogens, and with insect damage across the on-farm propagation cycles in the agroecological settings present at the altitudes at which plots experiments were planted. We also describe the difference in yield associated with the on-farm propagation cycles in different agroecological settings as an expression of seed degeneration.

Viruses Agroecological settings at the altitudes at which the plot experiments were conducted and the number of on-farm propagation cycles affected the percentage of seed samples infected

with viruses. The seed planted below 3000 m asl produced seed tubers showing higher percentages of viral infection in every on-farm propagation cycle ($p < 0.05$) (Fig. 5A). The percentages of seed samples infected with viruses were low and not significantly different in each on-farm propagation cycle for plots planted at and above 3000 m asl ($p > 0.05$) (Fig. 5A). In the experimental plots located below 3000 m asl, the beta regression estimated an average increase of 35.5% on the percentage of seed samples infected with viruses per on-farm propagation cycle. In contrast, at and above 3000 m asl, the beta regression estimated a lower average increase of 2.5% and 0.5% per on-farm propagation cycle on the percentage of seed samples with virus, respectively (Fig. 5A).

Other pathogens The percentage of seed samples infected with other pathogens was affected by the altitude at which the experiments were conducted and the on-farm propagation cycles (Fig. 5B). During cycle 1, the percentage of seed samples infected with other pathogens was not significantly different for the three altitudes (mean_{cycle1} = 15.4%, standard deviation (sd) = 11.3) (Fig. 5B). However, the percentage of seed samples infected with other

pathogens differed between altitudes in cycles 2 and 3 ($p < 0.05$). During these cycles, plots planted below and at 3000 m asl showed similar percentages of seed samples infected with other pathogens (mean_{cycle2} = 64.2%, mean_{cycle3} = 77.2%) ($p > 0.05$), but these percentages were significantly higher than those registered above 3000 m asl (mean_{cycle2} = 40.5%, mean_{cycle3} = 25.3%; $p < 0.05$). Our results showed that, below and at 3000 m asl, the percentage of seed samples infected with other pathogens could increase by an average of 22.0% and 33.0% per on-farm propagation cycle, respectively (Fig. 5B). However, above 3000 m asl, the trend of the percentage of seed samples infected with other pathogens could be uncertain as shown by the variability of the data.

Insect damage The agroecological settings present at the altitude at which the experiments were conducted and the number of on-farm propagation cycles influenced the percentage of seed samples with insect damage (Fig. 5C). At the three altitudes, the percentages of seed samples with insect damage were fairly high and similar during the first two on-farm propagation cycles (mean_{cycle1} = 84%, mean_{cycle2} = 87%; $p > 0.05$). However, in cycle 3, the percentage of seed samples with insect damage was higher above 3000 m asl (99%) in comparison with the plots planted below and at 3000 m asl (mean = 38.6%, sd = 18.8) ($p < 0.05$) (Fig. 5C). Our results showed a decline in the percentage of seed samples with insect damage in experiments below and at 3000

m asl at a rate of 30.5% and 18.5% per cycle, respectively. However, in the experiment above 3000 m asl, our results showed a slight increase (8.5% per on-farm propagation cycle) in the percentage of seed samples with insect damage ($p > 0.05$).

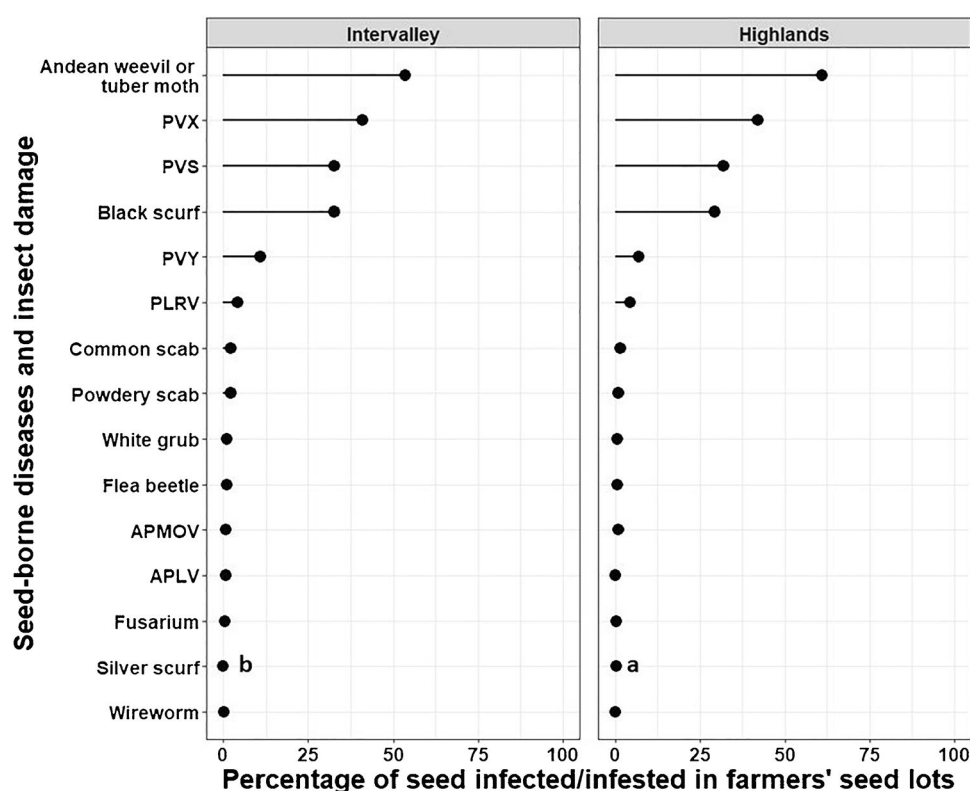
Yield Yield declined across the on-farm propagation cycles. This decline was associated with the agroecological settings present at the altitudes at which the experiments were conducted. The average yield below 3000 m asl was 17.4 t ha⁻¹, at 3000 m asl 25.3 t ha⁻¹, and above 3000 m asl 26.2 t ha⁻¹ (Fig. 5D). In experiments conducted below 3000 m asl, yield declined at an average rate of 8.4 t ha⁻¹ per on-farm propagation cycle. In plots planted at 3000 m asl, a decline was not clearly observed as yield was variable in each on-farm propagation cycle. In plots planted above 3000 m asl, yield declined at an average rate of 4.5 t ha⁻¹ per cycle.

3.2 Seed degeneration in the farmers' seed study

3.2.1 Incidence of bacterial, fungal, and viral diseases and insect damage

The results of our study showed that seed damaged by the Andean potato weevil or the tuber moth, or seed infected with PVX, PVS, and black scurf, was constantly identified in both agroecological settings in the province of Cotopaxi (Fig. 6). We found no difference in the incidence of seed

Fig. 6 Percentage of seed infected with diseases and insect damage in farmers' seed lots collected from the intervalley and the highlands. Letters (a, b) indicate significant differences at the 0.05 level between agroecological settings. Absence of letters indicates no significant difference.



damaged by the Andean weevil or the tuber moth, seed infected with black scurf, or seed infected with PVX and PVS between agroecological settings ($p > 0.05$) (Fig. 6). In the farms located in the intervalley, the damage attributed to the Andean weevil or the tuber moth predominated on the seed (mean = 53.6% of affected seed lots). This damage was followed by seeds infected with PVX (mean incidence = 41.0%), PVS (mean incidence = 32.6%), and black scurf (mean incidence = 32.6%) (Fig. 6). In the intervalley, we did not observe any presence of silver scurf (*Helminthosporium solani*) on the farmers' seed lots.

In the farms located in the highlands, the damage attributed to the Andean weevil and the tuber moth was high (mean incidence = 61.0%). Furthermore, seeds infected with PVX and PVS were found frequently, with average incidences of 42.0% and 32.1%, respectively. Black scurf was less frequently found in comparison with PVX and PVS, but there was still a high incidence (mean = 29.5%) ($p < 0.05$; Fig. 6). The presence of silver scurf was significantly higher in the highlands than in the intervalley ($p < 0.05$; Fig. 6). Yet, seed tubers with this disease were rarely found. We also identified several phytosanitary problems in less than 1% of the seed, for example, powdery scab (*Spongospora subterranea*), fusarium (*Fusarium* sp.), white grub (*Phyllophaga* spp.), or flea beetle (*Epitrix* sp.) (Fig. 6). We did not find wireworms' (*Agriotes* spp.) damage in the seed lots collected in the highlands.

3.2.2 Seed degeneration observed in the farmers' seed study

In this section, we describe seed degeneration in the two agroecological settings as the change in percentage of seed tubers infected with viruses, infected with other pathogens, and with insect damage in relation to the number of on-farm propagation cycles of those seed tubers. In addition, we describe the yield reported by farmers across these categories of the number of on-farm propagation cycles as an expression of seed degeneration in the two agroecological settings.

Viruses The percentage of seed infected with viruses was not influenced by the agroecological settings of the farms ($p > 0.05$) (Fig. 7A). Overall, the average percentage of seed infected with viruses was for the highlands 65.8% and the intervalley 70.8%. The categories of the number of on-farm propagation cycles did not significantly explain the variation in the percentage of seed infected with viruses either ($p > 0.05$) (Fig. 7A). Seed lots maintained by farmers for more than 10 years had the lowest percentage of seed infected with viruses (mean = 60.7%), whereas the seed lots maintained between 3 and 10 years had the highest percentage of seed infected with viruses (mean = 71.4%).

Other pathogens The percentage of seed tubers infected with other pathogens was not significantly different between the seed lots collected in the intervalley and the highlands ($p > 0.05$) (Fig. 7B). The lowest percentage of seed infected with other pathogens was found in the seed lots collected in the highlands (mean = 31.7%); it was slightly higher in the intervalley seed lots (mean = 36.2%). Moreover, we did not find a significant difference between seed lots obtained after the different numbers of on-farm propagation cycles ($p > 0.05$) (Fig. 7B). Overall, seed lots maintained for more than 10 years had the lowest percentage of seed infected with other pathogens (mean = 30.8%), whereas the seed lots maintained between 3 and 10 years had the highest percentage of seed infected with other pathogens (mean = 36.7%).

Insect damage The agroecological settings of the intervalley and the highlands and the categories of the number of on-farm propagation cycles did not influence the percentage of seed tubers with insect damage ($p > 0.05$) (Fig. 7C). This insect damage could be caused by different insects such as the Andean weevil, wireworms, or the white grub. In the highlands, the average percentage of seed with insect damage was 62.2%. It was slightly lower, but not significantly different, in the seed lots collected from the intervalley (mean = 55.8%). When the number of on-farm propagation cycles was compared, seed lots maintained by farmers between 3 and 10 years had the lowest percentage of seed with insect damage (mean = 52.9%), and the seed lots maintained by farmers between 1 and 3 years had the highest percentage of seed with insect damage (mean = 67.7%).

Yield Yield was not associated with the agroecological settings, the categories of the number of on-farm propagation, the percentage of seed infected with virus and other pathogens, or the percentage of seed with insect damage ($p > 0.05$; Fig. 7D). The yield reported by farmers in the highlands was slightly higher (mean = 10.0 bags of 45.45 kg harvested per 45.45-kg bag planted), but not significantly different, than the yield reported by farmers in the intervalley (mean = 9.6 bags of 45.45 kg harvested per 45.45-kg bag planted). Farmers maintaining their seed between 3 and 10 years reported higher yields (mean = 11.1 bags of 45.45 kg harvested per 45.45-kg bag planted), whereas the lowest yield was achieved when farmers kept their seed between 1 and 3 years (mean = 8.2 bags of 45.45 kg harvested per 45.45-kg bag planted) (Fig. 7D).

4 Discussion

The definition of seed degeneration suggests a yield reduction depending on the accumulation of seed-borne diseases or pests over successive on-farm propagation cycles (Struik and Wiersema 1999; Thomas-Sharma et al. 2016). The end result

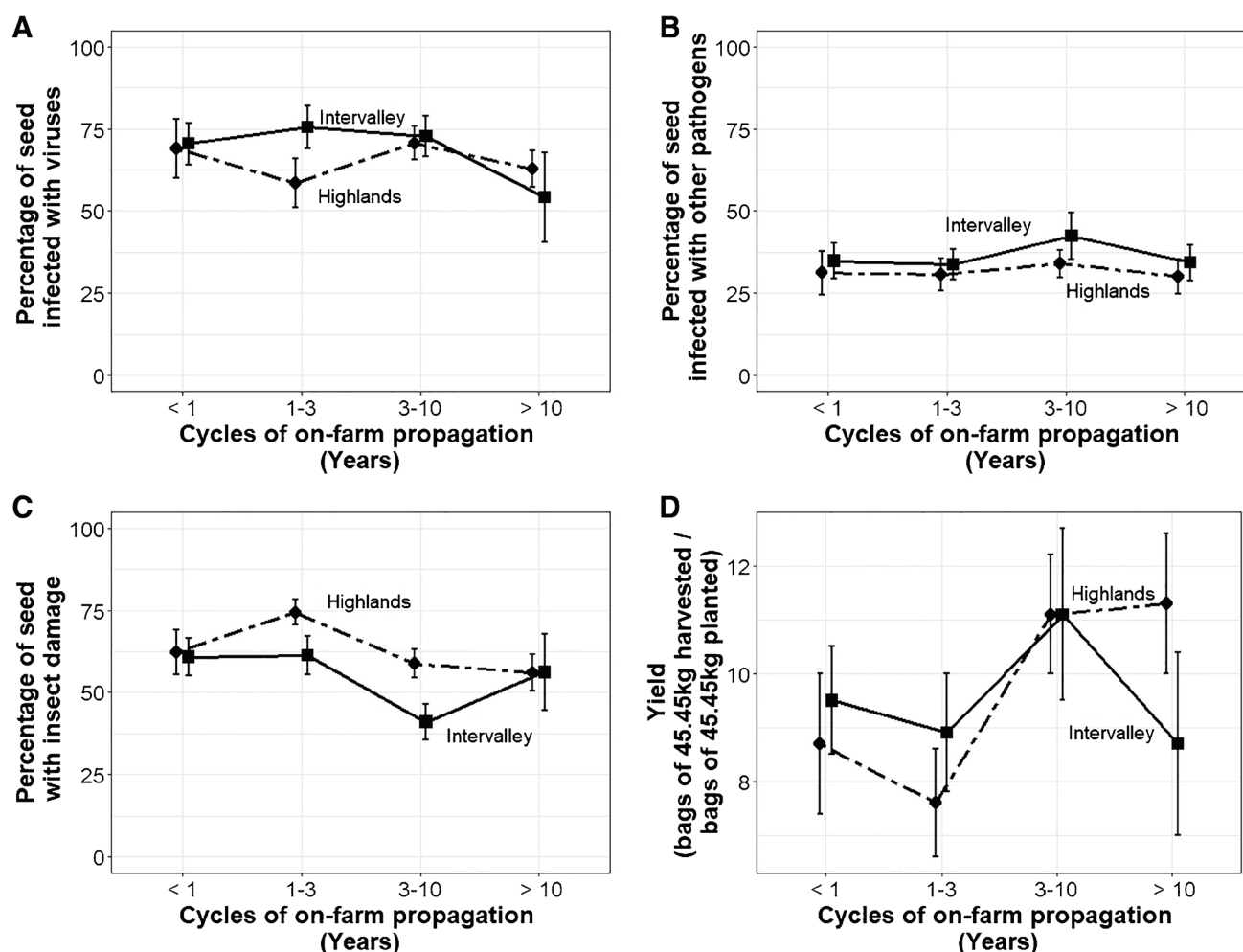


Fig. 7 Percentage of seed tubers infected with seed-borne diseases and insect damage in farmers' seed lots and yield over an increasing number of on-farm propagation cycles in farmers' fields. **A** Percentage of seed infected with viruses ($n = 191$ seed lots evaluated; total number of seed tubers evaluated: 1848). **B** Percentage of seed

infected with pathogens other than viruses ($n = 245$ seed lots evaluated; total number of seed tubers evaluated: 2931). **C** Percentage of seed with insect damage ($n = 245$ seed lots evaluated; total number of seed tubers evaluated: 2931). **D** Yield reported by farmers ($n = 260$ households' responses). Bars represent standard errors.

of the degeneration process is hypothesized to depend on the influence of the agroecological settings and the genetic resistance of the host (Thomas-Sharma et al. 2017). Our results confirmed that agroecological settings and the number of on-farm propagation cycles affect the percentage of seed infected with viruses and other pathogens, and the variation in seed with insect damage. However, this confirmation holds true only under experimental conditions. Under farmers' conditions, neither the agroecological settings nor the number of on-farm propagation cycles clearly affected the accumulation of diseases or pests on the seed. We discuss in more detail our results as follows: (1) the presence of seed-borne diseases and pests in the tropical highlands (i.e., mountainous areas present in the tropics) of Ecuador; (2) effects of agroecological settings and the number of on-farm propagation cycles on the percentage of seed infected with viruses, infected with other pathogens,

and with insect damage; and (3) yield differences associated with seed degeneration. Finally, we present the implications of our findings for the design and implementation of future seed system interventions.

4.1 Presence of seed-borne diseases and pests in the tropical highlands of Ecuador

The results of our experimental plots and farmers' seed study showed that potato seed lots were frequently affected by the Andean weevil or the tuber moth and black scurf (Figs. 4 and 6). Similar findings were reported by Fankhauser (2000) and Navarrete et al. (2017) in Ecuador. The importance of these seed-borne pests is highlighted not only in our findings but also by Ecuadorian farmers' concerns, given that they

recognize these problems as part of the set of causes of seed degeneration (Buddenhagen et al. 2017).

Our results indicated that seed-borne pathogens and pests had a different behaviour depending on the agroecological settings studied. Agroecological settings were associated with changes in the incidence of seed damaged by the Andean weevil or the tuber moth, particularly in the multi-annual field experiment (Fig. 4). We expected these results, as the Andean weevil is predominant in environments above 3000 m asl (Alcázar and Cisneros 1999; Kühne et al. 2007), and the tuber moth in environments below 3400 m asl (Dangles et al. 2008; Kroschel and Schaub 2013). This different behaviour was not the case for the incidence of farmers' seed infected with PVX and PVS. Similar incidences of both viruses were found in previous studies in Ecuador (Navarrete et al. 2017) and Peru (above 3000 m asl) (Kreuze et al. 2020). We found that there was a low presence of seed infected with PVY and PLRV, confirming results of other studies that investigated the incidence of these viruses in agroecological settings above 3000 m asl (Navarrete et al. 2017; Scurrah et al. 2009).

Unravelling the relation between the behaviour of seed-borne pathogens and pests and agroecological settings is also important for the management of new seed-borne diseases and pests causing seed degeneration. In Ecuador, there are four new potential causes of seed degeneration associated with purple top disease that were not looked for during our studies. These are the following: (1) the bacterium *Candidatus Liberibacter solanacearum* (causal agent of zebra chip; Caicedo et al. 2020), (2) the phytoplasma *Candidatus Phytoplasma aurentifolia* S16rII (Caicedo et al. 2015), (3) the phytoplasma *Candidatus Phytoplasma* [aster yellow cluster, ribosomal subgroup 16SrI-F] (Castillo et al. 2018), and (4) the potato psyllid (*Bactericera cockerelli*; Castillo et al. 2019). However, it remains unknown how these four new potential causes of seed degeneration associate or behave under the different agroecological settings present in Ecuador.

Our results and the information of previous studies, together, highlight the importance of understanding the role of agroecological settings on the development and establishment of plant diseases and pests (Bertschinger 1992; Scholthof 2007).

4.2 Effects of agroecological settings and the number of propagation cycles on the percentage of seed infected with viruses, infected with other pathogens, and with insect damage

In the multi-annual field experiment, there was an increase in the percentage of seed samples infected with viruses and other pathogens over the number of propagation cycles. However, this increase depended on the agroecological settings present at the altitudes at which the experimental plots

were planted (Fig. 5A and B). Higher rates of increase were found at lower altitudes, and lower rates of increase were found at higher altitudes. Bertschinger (1992) and Luque et al. (1991) found similar results for viruses in Peru and Colombia, respectively. Previous experiments performed in Ecuador support our findings that the increases in percentage of seed infected with virus were negligible above 2800 m asl (Fankhauser 2000). Our results also show that there was a relationship between the percentage of seed samples with insect damage and agroecological settings present at the altitudes at which the experimental plots were planted (Fig. 5C). However, the rates (increase or decline) were more variable than for viruses and other pathogens.

However, the results from our farmers' seed study challenge those found in our multi-annual field experiment. Here, neither the agroecological settings nor the number of on-farm propagation cycles influenced the percentage of seed infected with viruses, seed infected with other pathogens, and seed with insect damage significantly (Fig. 7A, B, and C). This difference in results could be explained by the farmers' seed management (Navarrete et al., 2022). In the farmers' seed study, local management practices, for example potato variety use, could have influenced the variation in seed infected with diseases or infested with insects. Selecting seed or performing positive selection by individual farmers could have reduced the percentage of seed infected with viruses (Priegnitz et al. 2019; Schulte-Geldermann et al. 2012). Other embedded practices could also contribute to the difference in results between the multi-annual field experiment and the farmers' seed study. In Cotopaxi, for example, the seed that farmers use could come from potatoes received as a gift (*ración*) or potato plots planted at different agroecological settings depending on their land availability and access.

The number of on-farm propagation cycles is normally used by extension agents or researchers to estimate the level of accumulation of diseases and pests in/on seed. The rule of thumb is that a seed lot that has been propagated for more than 3 years should be replaced due to seed degeneration (first author's personal observation). Even we started this project expecting to be able to make a recommendation to farmers about the number of cycles during which they should propagate their seed. This idea was confirmed by our results obtained in the multi-annual field experiment (Fig. 5A, B, and C) but challenged by our findings from the farmers' seed study (Fig. 7A, B, and C). We now hypothesize that, under farmers' conditions, the number of vegetative propagation cycles could be a proxy for the accumulation of diseases and pests and also an indicator of farmers' capacity (knowledge and practices) to maintain a tolerable level of diseases and pests on their seed and obtain an acceptable yield. The results of our multi-annual field experiment show that indeed on-farm propagation cycles could be a useful

proxy for the accumulation of seed-borne diseases and pests depending on the agroecological settings (Fig. 5A, B, and C). The results of our farmers' seed study complement the second part of our hypothesis. These results show that when farmers produce the seed, seed lots do not necessarily degenerate, and yield does not surely decline over the cycles of on-farm propagation (Fig. 7). These findings suggest that some farmers in the Andes have the capacity to maintain their seed at a certain quality as their practices have an influence on seed degeneration and yield (Navarrete et al., 2022). The second part of our hypothesis is also supported by the literature on seed replacement since most farmers take care of their seed and are aware of its importance, but replace their seed—not the variety—when they observe low yields (Crissman et al. 1993; Monares 1988a, 1988b; Thiele 1999; Zeven 1999). Consequently, farmers will keep their seed as long as the crop meets their expectations. Testing how farmers' practices interact with seed performance will help identify opportunities for extending seed performance over more cycles of on-farm propagation. Every additional on-farm propagation cycle could help farmers save money that they would otherwise have to spend on seed.

4.3 Yield variation associated with seed degeneration

The results from our multi-annual field experiment showed that the agroecological settings present at the altitudes at which the experiments were conducted and the number of propagation cycles were associated with yield decline (Fig. 5D). We found that the yield declined faster in experimental plots planted below 3000 m asl (rate = 8.4 t ha⁻¹ per cycle) than above 3000 m asl (rate = 4.5 t ha⁻¹ per cycle). Unfortunately, because of the low number of observations in the experiments, we were unable to correlate yield with the percentage of seed samples infected with diseases and pests. The results of the farmers' seed study, however, contrast sharply with those found in the multi-annual field experiment. We did not find farmers' yields being associated with the percentage of seed infected with viruses, the percentage of seed infected with other pathogens, the percentage of seed with insect damage, the number of on-farm propagation cycles, and the agroecological settings ($p > 0.05$) (Fig. 7D). As low yields are still predominant in the Andean region, our results suggest that there are other limiting factors in Ecuador (e.g., water and nutrient deficiency, late blight, purple top, or nematodes). It is critical to identify these other yield-limiting factors to design on-farm management practices that, in combination with high-quality seed, will lead to improved potato productivity (Fermont et al. 2009; Haverkort and Struik 2015).

Although we do not want to minimize the value of asking farmers about their yields during the surveys, we would

like to acknowledge that it might be a potential limitation of this research. These data could be imprecise because farmers might not remember accurately. Direct methods could have been used to measure yields during our survey, such as harvesting a determined number of plants or area and later performing calculations to estimate yield (Sapkota et al. 2016). We suggest that our results be taken cautiously and that future investigations measure yield directly to obtain more accurate estimates about the effect of seed-borne diseases and pests on yield (Beegle et al. 2011; Fraval et al. 2019; Sapkota et al. 2016).

4.4 Take-home messages for seed system interventions

We derived three take-home messages from performing this research in the tropical highlands of Ecuador. The first one is that many seed-borne diseases and pests affect potato seed quality. Future seed interventions should understand why certain diseases and pests are present in high percentages on/in the seed (Figs. 4 and 6). It could be that farmers have limited capacity to manage these problems, are not aware of the problems infecting/infesting their seed (Fig. 6), or are not perceiving the losses in yield associated with seed-borne diseases and pest (Fig. 7D) as important enough to manage them. Seed interventions should build on this new understanding to strengthen farmers' capacities to identify and manage seed-borne diseases and pests such as the Andean weevil and the tuber moth (Figs. 4 and 6). These interventions should also raise awareness and provide training about the potential new causes of seed degeneration, as in the case of Ecuador, the potential causal agents of purple top disease.

The second take-home message is that we need to understand better the relationship between agroecological settings and the presence of seed-borne diseases and pests and seed degeneration. This will help design a portfolio of options depending on the context (Nelson et al. 2016). At the same time, future interventions should examine and be based on the interaction of local seed management practices with agroecological settings and seed-borne diseases and pests.

The last take-home message is that the number of on-farm propagation cycles under farmers' conditions could be both an expression of the accumulation of seed-borne diseases and pests and of the farmers' ability to maintain the quality of their seed — and of their interaction. Our suggestion is that, before recommendations are provided about seed replacement, potato seed degeneration in the area of interest should be studied. These new studies need to investigate the process of seed degeneration not only in a research station, but also in farmers' fields where there are different agroecological settings, management practices, and potato varieties. Other approaches are currently available to support the improvement of potato seed management

recommendations (e.g., implementation of positive selection), such as the use of models to understand the effect of interventions like seed replacement on seed degeneration (Thomas-Sharma et al. 2017) or to understand how to distribute high-quality seed most effectively through farmers' exchange networks to reduce the impacts of seed-borne diseases (Garrett 2021).

5 Conclusions

We conclude that potato seed degeneration in the Andes is a process that depends on agroecological settings and the number of on-farm propagation cycles. However, this was observed only under experimental conditions. In the farmers' settings, the influence of these factors was not significantly accounting for the variation in the percentage of infected/infested seeds and yield. These results suggest that both agroecological settings and on-farm propagation cycles explain seed degeneration only partially. Other, unexplored, factors could play an important role in farmers' settings, such as local seed management, e.g., seed tuber selection and potato variety use. This implies that it is necessary to venture outside research stations to study seed degeneration. Understanding what farmers and extension agents know, or do not know, about seed-borne diseases and pests, and understanding in collaboration with farmers the role of agroecological settings and the potential effects of the number of on-farm propagation cycles in seed degeneration could be important first steps. Future seed system interventions should take into consideration the potential variety of unidentified yield-limiting factors. To improve the productivity of potato farmers, it is pivotal to identify and potentially improve the most significant yield-reducing factors before farmers are advised to invest in expensive seed management practices, for example, high-quality seed. We expect that the results presented in this paper will contribute to understanding potato seed degeneration in the Andes, the development of seed potato sectors, and the design of seed interventions.

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Authors' contributions I. Navarrete designed and performed the research, collected and analysed the data, and led the writing of the manuscript. V. López supported the data collection and assisted with the interpretation of the information and the writing of the manuscript. C.J.M. Almekinders, J.L. Andrade-Piedra, P. Kromann, and P.C. Struik assisted with the design, analysis, and interpretation of the information and assisted with the writing of the manuscript. All of the authors reviewed the manuscript critically and approved the submitted version.

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Data availability All the raw data used in this manuscript is stored in Dataverse. The raw data of the experiments is available in Kromann et al. (2017), and the raw data of the farmers' seed study is in Navarrete et al. (2018, 2019).

Code availability Not applicable

Declarations

Ethics approval Not applicable

Consent to participate Participants gave oral consent to use the information.

Consent for publication Participants gave oral consent to use the information.

Conflict of interest The authors declare no competing interests.

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