ORIGINAL ARTICLE

Damage quantification in *Physalis peruviana* L. infected by the new putative sobemovirus physalis rugose mosaic virus

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Abstract

A putative new virus, physalis rugose mosaic virus (PhyRMV), has been reported more frequently in *Physalis peruviana* associated with severe symptoms. In this study the damage caused by sap-inoculated PhyRMV in *P. peruviana* was assessed based on the comparison of host vegetative and reproductive parameters between virus-infected and healthy plants. Infected plants confirmed using molecular assays, showed a reduction in growth, leaf area, specific leaf area (SLA) and relative chlorophyll content. PhyRMV-infected plants yielded 70% less fruit of general lower quality parameters, except for pH, compared with the healty plants. Finally, seeds from PhyRMV-infected plants showed a reduced germination rate and, in accelerated aging assay, vigor of seeds were also significantly reduced.

Introduction

The cape gooseberry (*Physalis peruviana* L.), member of the Solanaceae family, is a shrub native to the Andean region of South America, that has increased in importance since the first commercial production in the 1980s in Colombia (Fischer and Miranda 2012; Fischer et al. 2014). Although *P. peruviana* was first cultivated in Brazil in 1999 and expanded throughout the highland regions of Santa Catarina and Rio Grande do Sul, it is still considered an emerging crop (Muniz et al. 2014). Such status is due to a lack of studies on crop development, especially with regard to the damage by viral diseases (Eiras et al. 2012; Fariña et al. 2018, 2019).

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Despite the documentation of several viruses infecting *P. peruviana* reported worldwide (Da Graça et al. 1985; Prakash et al. 1988; Thomas and Hassan 2002; Salamon and Palkovics 2005; Trenado et al. 2007; Gámez-Jiménez et al. 2009; Perea et al. 2010; Aguirre-Ráquira et al. 2014; Gutiérrez et al. 2015; Kisten et al. 2016), only three viruses are known to infect *P. peruviana* in Brazil. Two of them belong to genus *Orthotospovirus*: 1) tomato chlorotic spot virus (TCSV), which was detected in the state of Rio Grande do Sul causing dwarfing, mosaic, necrosis, and leaf distortion (Eiras et al. 2012), and 2) groundnut ring spot virus (GRSV), which is known to cause chlorotic spots and concentric rings on the leaves (Fariña et al. 2018). In addition, a new putative sobemovirus named physalis rugose mosaic virus (PhyRMV) was discovered at a high incidence in the states of Santa Catarina, Paraná, and São Paulo, where commercial production is concentrated. Plants infected with PhyRMV showed mosaic, reticulated mosaic, yellowing, leaf crinkle, and dwarfing (Fariña et al. 2019).

Considering the limited information about this new sobemovirus, as well as the expansion of *P. peruviana* cultivation in Brazil, it is fundamental to increase the understanding of the effects caused by viral infection on the host. Our findings presented may provide insights useful in case the disease further spread into other countries that grow *P. peruviana* commercially. Our main objective was to

quantify the damage due to viral infection on both vegetative and reproductive parameters of plant growth.

Materials and methods

Virus inoculation and molecular detection of PhyRMV

Physalis peruviana seedlings with two completely expanded leaves were grown from seeds and transplanted into 18 vessels. Plants were cultivated under a V-conduction system under greenhouse conditions at 24 °C (± 2 °C). After 25 days, nine plants were mechanically inoculated with PhyRMV isolate from Lages/ Santa Catarina. This isolate was obtained from a *P. peruviana* production area and it is maintained through mechanical inoculation in a greenhouse. No additional viral infection was confirmed using biological and molecular tests (Fariña et al. 2019). Nine plants were mock-inoculated with extraction buffer (0.05 M sodium phosphate and 0.02 M sodium sulfite, pH 7.0) and constituted the non-infected or healthy control plants.

For molecular analysis, symptomatic *P. peruviana* leaves were homogenized in liquid nitrogen and submitted to total RNA extraction using TRI reagent (Sigma Aldrich) following the manufacturer's instructions. For cDNA synthesis, SuperScript III-Reverse transcriptase (Invitrogen) enzyme was used following the manufacturer's instructions, and polymerase chain reaction (PCR) was carried out using TaKaRa Taq™ DNA Polymerase (Clontech) following the manufacturer's instructions. Confirmation of PhyRMV presence in plants inoculated with buffered plant extract was performed using specific primers Sobemo1F 5'-TAGCCAAGCTCAATCCATTT-3′ and Sobemo1R 5'-GTCTTAGGCCAAGAAGTCAA-3′, which allows amplification of a 528 bp fragment of the polymerase gene, at an annealing temperature of 53 °C for 1 min (Fariña et al. 2019). Mother plants and plants used in the experiments were also tested using universal primers for begomoviruses (Rojas et al. 1993), potyviruses (Zheng et al. 2009), sobemoviruses (Arthur et al. 2010), tobamoviruses (Heinze et al. 2006), and tospoviruses (Eiras et al. 2001).

All PCR products were submitted to agarose gel electrophoresis (1.0%), stained with GelRed (Biotium), and vizualised with UV light. Amplified DNA fragments of the expected size were purified using Axy prep (Axygen) purification kit, following manufacturer's instructions, sequenced and queried against NCBI database using the BLASTn and BLASTx search tools with standard parameters.

Virus infection effect on host growth

Beginning at 25 days after inoculation (DAI) plant height was measured along the main stem. Leaf area was estimated following the method used by Bianco et al. (1983), using the width and length (W × L) of the youngest, completely expanded leaves. These measurements were used with the following equation: $Y = 0.58763(W \times L) + 2.575$, where Y is the estimated leaf area obtained through linear regression of the real leaf area of 60 *P. peruviana* leaves.

Relative chlorophyll was measured from six random readings (one reading per leaf) using a Soil-Plant Analyses Development (SPAD) SPAD - 502 device (Konica-Minolta). To determine if the SPAD index value of infected plants is related to higher photosynthetic rate, two parameter evaluations related to gas exchange and chlorophyll A fluorescence (at 80 and 111 DAI) were carried out in healthy and PhyRMV-infected plants. Photosynthesis parameters [photosynthesis (A), transpiration rate (E), stomatal conductance (gs), electron transport rate (ETR) and quantum yield for photochemical energy conversion in photosystem II (ΦPSII)] were measured using a LI-6400XT (LI-COR Biosciences) portable meter equipped with a fluorescence integrated chamber from five random readings on each treatment. Actinic lighting was used at 800 μmol m^{-2} s^{-1} with 10% blue light, and CO_2 concentrations varied between 410 and 440 μmol mol^{-1}. Electron transport rates and ΦPSII were measured under stable actinic light conditions. For specific leaf area (SLA) measurements, 30 leaves per treatment were assessed using a LI-300C leaf area integrator (LI-COR Biosciences). After measurements were taken, leaves were dried at 65 °C for 72 h and weighed, and the mass of each leaf was divided by its corresponding area. Plant height, leaf area, and SPAD index value were measured every 14 days (beginning at 24 DAI), completing nine evaluations. Photosynthesis parameters were measured at 80 and 111 DAI, and SLA was evaluated at 152 DAI.

Virus infection effect on fruit yield and quality

Fruits were harvested manually twice a week, between 98 and 152 DAI, at maturation stage 4 in accordance with Colombian Technical Standard No. 4580 of 1999 of the Colombian Institute of Technical Standards. The harvested fruits were separated into two treatments (healthy and infected plants), with each replication containing six fruits. Average number of fruits, berry weight (g), berry diameter (mm), pH, soluble solids content (Brix), and titratable acidity (citric acid %) were analyzed. Berry weight was obtained using a digital scale (Bel Engineering Mark s3102) with precision of 0.05 g. Berry diameter was determined using a 6″ digital pachymeter (Zaas Precision) (0 a 150 mm), through averaging six measurements of each berry for both replicates.

Physicochemical analyses were performed using the fruit content of each treatment. Potential hydrogen (pH) was measured using a digital pH meter (ION pHB 500), and soluble solid content was obtained by refractometry with a temperature correction of 20 °C. For titratable acidity, a sample

containing 50% of *P. peruviana* juice was titrated using 0.1 N NaOH.

Virus infection effect on seed quality

To evaluate the influence of viral infection on seed quality, germination, emergence speed index (ESI) value, and vigor tests after accelerated aging were performed. The seeds used in the experiment were kept in sealed tubes for thirty days at 5 °C (Muniz et al. 2014).

In germination tests, performed at 21 days after sowing (DAS) (Brasil 2009), four replicates of 100 seeds were used for each treatment. Seeds were distributed in germination boxes with blotting paper moistened with 2.5 times the weight of the dry paper of 0.2% KNO₃ saline solution in a seed germinator at 25 °C.

For ESI, 200 seeds were used for each treatment in four subsamples of 50 seeds (Maguire 1962). Seeds were sown manually in a greenhouse using plastic trays (42 × 26 cm) containing a soil/substrate mixture (3:1), to a depth of 3 mm.

Daily observations were made on the seedlings that emerged from the first to 28 DAS. The ESI value was determined by dividing the sum of the number of normal seedlings that emerged daily by the number of days elapsed between sowing and emergence based on Maguire's formula (Maguire 1962). The primary root and shoot length of seedlings were measured at 28 DAS.

Accelerated aging was conducted in two modified germination boxes containing two compartments divided by a tissue paper, with one of the boxes containing 40 mL saturated NaCl solution (40 g of NaCl in 100 mL of water) (Jianhua and Mcdonald 1996; Marcos-Filho 2015) and a control box containing distilled water. Eight hundred seeds were deposited on the tissue paper in each box. The boxes were kept at 41 °C and were evaluated after 48 and 72 h. To evaluate vigor, four subsamples of 100 seeds from each box were subjected to germination testing, and only normal seedlings were used. Normal seedlings are well developed, complete, and healthy. The vigor (germination % in accelerated aging condition) and primary root and shoot length were evaluated at 14 DAS.

Statistical analyses

A completely randomized design was used in all experiments, and statistical analyses were performed using R software (version 3.5.1). The homocesdacity and normality weres checked using the F-snedecor and Shapiro–Wilk tests, respectively. When both conditions could be assumed, t-tests were used for two group comparison, otherwise the Wilcoxon–Mann–Withney test was used. For seed health experiments means were compared using F-test.

Results

Detection of the virus in inoculated plants

All inoculated plants showed typical symptoms of PhyRMV infection and were positive in RT-PCR assays. Infection by other viruses was tested, but no fragments were amplified, except with universal primers for sobemoviruses (data not shown).

Viral infection effect on plant growth and development

Both vegetative and reproductive phases of plant development were affected by PhyRMV infection. However, photosynthetic parameters showed no significant differences between healthy and infected plants [for 80DAI: P values = 0.3 (A), 0.79 (E), 0.66 (gs), 0.09 (ETR) and 0.17 (ΦPSII); for 111DAI: P values = 0.068 (A), 0.55 (E), 0.14 (gs), 0.75 (ETR) and 0.72 (ΦPSII)]. For plant height, differences could be measured up to 94 DAI [P-values = 0.0025 (24DAI), 0.0007 (38 DAI), 0.0004 (52 DAI), <0.0001 (66 DAI), 0.0002 (80 DAI) and 0.02 (94 DAI)]. After this period, no differences were recorded [P-values = 0.14 (108DAI), 0.82 (122 DAI), 0.53 (136 DAI) and 0.31 (150 DAI)]. Additionally, a significant reduction in leaf area of infected plants was observed during all evaluations [P-values = 0.0004 (24DAI), <0.0001 (38 DAI), <0.0001 (52 DAI), <0.0001 (66 DAI), 0.0008 (80 DAI), <0.0001 (94 DAI), 0.0004 (108DAI), 0.03 (122 DAI), 0.008 (136 DAI) and 0.004 (150 DAI)]. The SLA values of infected plants varied from 221 to 1570.2 cm²/g, while the highest value recorded in healthy plants was 276.64 cm²/g, demonstrating a significantly lower ($P < 0.0001$) accumulation of dry mass in infected plants. There is a region between 221 and 276 cm²/g where diseased and healthy controls overlap. The overlap occurred because the leaves from infected plants presented variation in the severity of symptoms, but it is noteworthy that differences based on the median and P value were statistically significant.

The SPAD index measured the relative chlorophyll content, and these data varied the most. In the first three evaluations (24, 38, and 52 DAI), higher rates were measured in healthy plants (43.49, 34.60, and 31.84, respectively). However, significant differences were not measured from 52 to 122 DAI, when higher values (31.74) were detected in infected plants. During subsequent evaluations (136 and 150 DAI), significant differences were not detected between the two treatments (Table 1). Neither gas exchange nor chlorophyll A fluorescence parameters showed any significant differences, indicating that the photosynthetic activity was not altered in *P. peruviana* infected with PhyRMV at 80 and 111 DAI.

Table 1 SPAD index values of *Physalis peruviana* leaves of healthy and PhyRMV-infected plants at increasing days after inoculation (DAI)

DAIs	SPAD Index values		CV (%)	*P*-value
	Healthy	PhyRMV-infected		
24 DAI[a]	43.49 ± 3.26	33.49 ± 3.99	16.22	<0.0001
38 DAI[a]	34.60 ± 3.87	29.16 ± 3.59	14.37	0.007
52 DAI[a]	31.84 ± 2.87	27.31 ± 2.92	12.34	0.004
66 DAI[a]	31.46 ± 3.62	29.53 ± 3.01	11.08	0.23
80 DAI[b]	28.81 ± 2.06	26.83 ± 4.10	11.89	0.48
94 DAI[a]	26.29 ± 2.73	27.78 ± 4.00	12.60	0.36
108 DAI[b]	25.52 ± 1.57	30.08 ± 4.47	14.43	0.06
122 DAI[b]	25.69 ± 1.89	31.74 ± 3.00	13.75	0.003
136 DAI[b]	27.84 ± 1.71	30.91 ± 3.98	11.84	0.11
150 DAI[b]	29.11 ± 3.74	31.16 ± 5.92	16.31	0.66

[a] Bilateral t-test for differences between sample means

[b] Wilcoxon-Mann-Whitney for the differences between sampled medians. CV, Coeficient of Variation. *P* values under 0.05 show significant differences between healthy and PhyRMV-infected plants

Virus infection influenced both yield and quality parameters of fruits. A 10-day delay in fruit harvest was observed in PhyRMV-infected plants, and fruits produced were malformed (Fig. 1). Each healthy plant produced 68 fruits on average, and infected plants produced 20 fruits on average, resulting in a 70% fruit yield reduction (Fig. 1). Larger differences were observed in fruit (calyx + berry + pedicle) weight,

with a 14% reduction in virus-infected plants. Reductions in berry diameter, solid soluble contents, and acidity of 8%, 5%, and 9.4% respectively, were also observed (Fig. 2). No significant differences were observed in pH values (Fig. 2).

Virus infection effect on seed quality

PhyRMV infection reduced the germination rate of *P. peruviana* seeds, with a significantly higher germination percentage of healthy seeds (90%) compared to the germination of seeds of infected plants (68%) ($P = 0.03$). However, no significant differences in primary root ($P = 0.68$) and shoot length ($P = 0.22$) of the developed seedlings were observed between seedlings of seeds from healthy and infected plants, indicating that PhyRMV does not reduce seed physiological potential (Table 2). No significant influence of PhyRMV on seed germination speed ($P = 0.22$), primary root ($P = 0.42$) and shoot length ($P = 0.92$) was recorded, supporting the results found in the germination test (Table 3).

Plant vigor was not affected by exposure times of 48 h and 72 h to saturated NaCl solution. However, significant differences were detected in the control plants at 72 h incubation in water, in which healthy seeds were significantly more vigorous (97%) compared to seeds from infected plants (76%) ($P = 0.013$). Primary root and shoot length showed significant differences at 72 h incubation in water ($P < 0.001$) or saturated NaCl solution ($P < 0.001$), with healthy seedlings showing higher values in both cases (Table 4).

Fig. 1 Visual appearance of fruits harvested from healthy (upper) and PhyRMV-infected plants (lower) (**a**), boxplot for the number of fruits harvested by week from healthy and PhyRMV-infected plants (**b**), differences between treatments were analyzed with Wilcoxon-Mann-Whitney test. Medians: 78.0 for Healthy and 18.0 for PhyRMV-Infected plants, P < 0.05: (Significant at 95% significance), and harvest at 125 days after inoculation (DAI) (C)
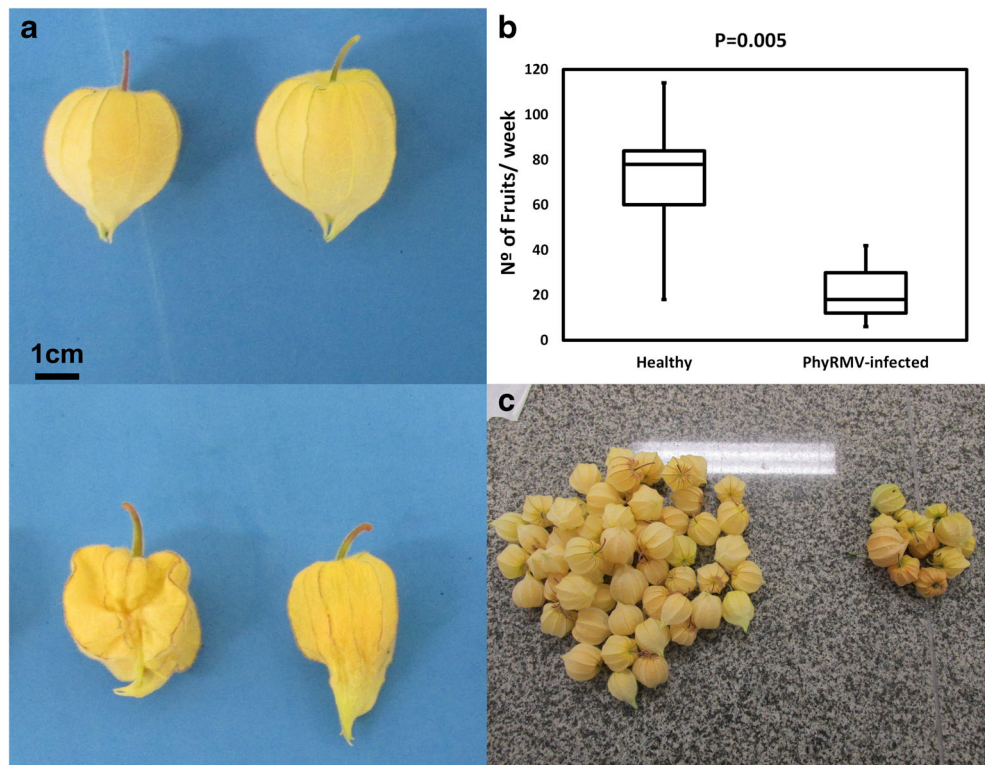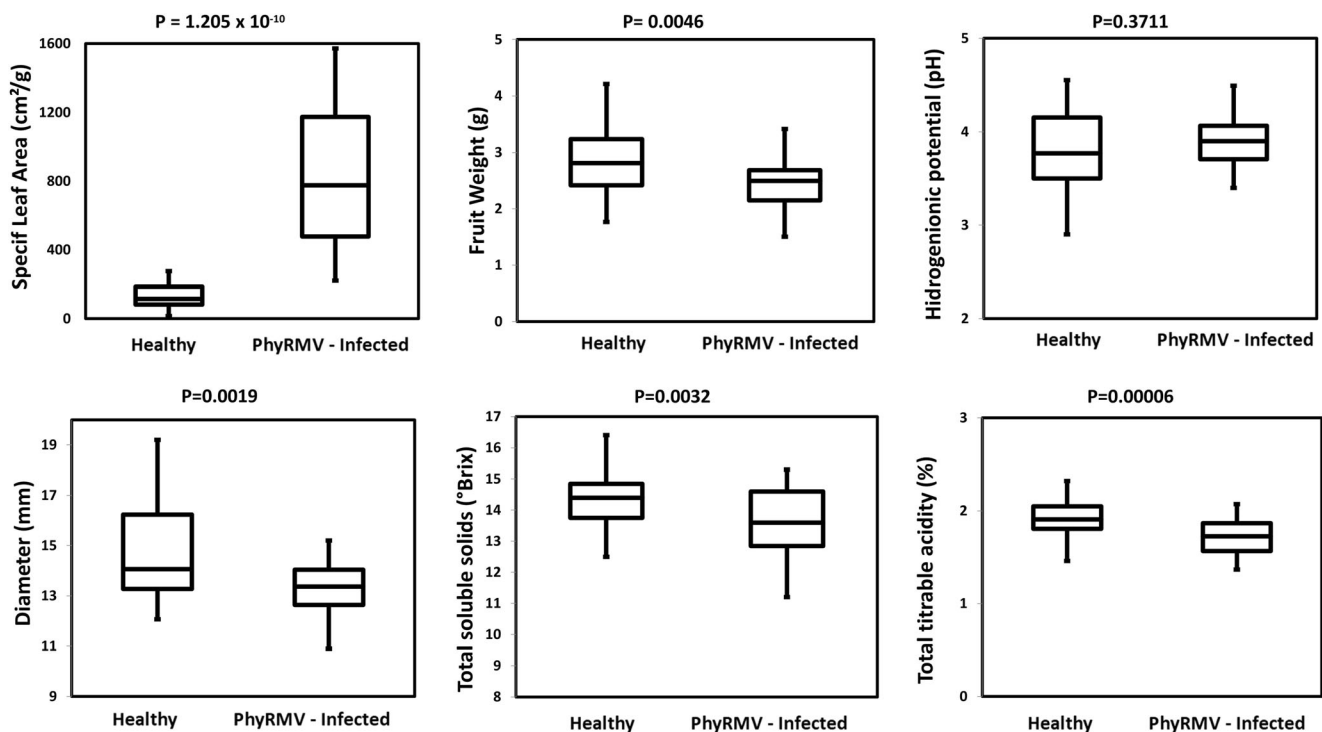
Fig. 2 Boxplots for specific leaf area and qualitative and quantitative parameters of *Physalis peruviana* fruits from healthy and PhyRMV-infected plants. Wilcoxon-Mann-Whitney test was used for leaf specific area, berry diameter, fruit mass (berry + chalice + tassel), and pH; bilateral t test for total soluble solids and total titratable acidity. $P < 0.05$: Significant at 95% significance; $P < 0.01$: significant at 1% significance

Discussion

Physalis rugose mosaic virus (PhyRMV) can affect *P. peruviana* on plant growth, development, fruit quality, and seed production. Based on the results presented here, viral infection likely interferes in chlorophyll production in mesophyll cells at least until the period that significant differences were observed. Altered chlorophyll production can be caused by several factors related to host physiology, such as (*i*) reduction of photosystem efficiency, (*ii*) reduction in chlorophyll amount, (*iii*) accumulation of photo assimilates in leaves, (*iv*) chloroplast morphologic alterations, and/or (*v*) changes in expression of photosynthesis related genes (Zhao et al. 2016). Rarely, sobemoviruses have been found to interact with chloroplasts, with the exceptions of southern bean mosaic virus (SBMV) and rice yellow mottle virus (RYMV), which cause degenerative changes in chloroplasts when viral particles were present in large amounts into the cell (Weintraub and

Ragetli 1970; Opalka et al. 1998; Brugidou et al. 2002). Additional analyses of photosynthetic activity during the early stages of infection are needed to elucidate the possible causes of chlorophyll reduction.

Reduction of chlorophyll content in virus-infected plants is common (Basso et al. 2010; Monteroa et al. 2016; Farooq et al. 2019). However, most studies considered a short period of time after infection. In this study, it was demonstrated that depending on the stage of the infection, the behavior can be variable, suggesting a recovery of chlorophyll content in PhRMV-infected plants as a compensation mechanism due to reduced leaf area. However, this compensation mechanism was not enough to ensure fruit production.

For sobemoviruses, similar studies have been performed for RYMV in rice (*Oryza sativa* L.) with yield reductions ranging from 10% to 100%, and subterranean clover mottle virus (SCMoV) afecting subterranean clover pastures in Australia, with reductions of 10% to 44% in yields (Jones

Table 2 Statistics for germination, primary root and primary shoot length of seedlings originated from seeds of healthy and PhyRMV-infected plants

Treatment	Germination rate (%)	Primary root length (mm)	Primary shoot length (mm)
Healthy	90 a	46.60 a	21.85 a
PhyRMV-infected	68 b	44.60 a	20.20 a
CV (%)	13.88	48.65	30.14

CV, Coeficient of Variation. Means followed by the same letter did not differ by F-test at 5% probability

Table 3 Emergence speed index (ESI), primary root and primary shoot length of seedlings originated from seeds of healthy and PhyRMV-infected plants

Treatment	ESI	Primary root length (mm)	Primary shoot length (mm)
Healthy	0.1945 a	49.26 a	34.13 a
PhyRMV infected	0.1661 a	48.81 a	39.53 a
CV (%)	16.51	16.30	28.51

CV, Coeficient of Variation. Means followed by the same letter did not differ by F-test at 5% probability

2013). Although there are extensive data on yield losses caused by viruses in solanaceous plants like tomato and pepper, there is no available information on *Physalis* spp. (Giordano et al. 2005; Péréfarres et al. 2012; Rocha et al. 2012; Sevik and Arli-Sokmen 2012; Barbosa et al. 2016). The data presented here (70% fruit yield reduction) are supported by the literature and demonstrate the importance of PhyRMV infections on yield reductions.

The drastic reduction in SLA and fruit production may also be related to viral cell-to-cell movement, which is mediated by the interaction of movement and coat proteins with plasmodesma. This, along with replication and concentration of virus in the phloem tissues, could result in cellular changes and tissue disorders, resulting in negative effects on photo assimilate translocation, which could lead to the accumulation of starch in leaves (Gonçalves et al. 2005; Basso et al. 2010). This accumulation could result in feedback inhibition, leading to symptoms associated with color change (Taiz and Zieger 2013). This hypothesis could be tested by quantifying starch concentrations in the leaves of healthy and PhyRMV-infected plants. Although, sobemoviruses are known to be transported long distance in both xylem and phloem (Sõmera et al. 2015), several of the economically important viruses, such as cocksfoot mottle virus (CfMV), SBMV and southern cowpea

mosaic virus (SCPMV), are transported only through the phloem (Weintraub and Ragetli 1970; Morales et al. 1995; Otsus et al. 2012). There is still no information on long-distance movement of PhyRMV, but it is reasonable to infer that the movement of the virus may be directly or indirectly involved in the damage measured.

The reduction in yield contributing components such as fruit weight caused by viruses is widely reported in the literature (Fletcher et al. 2000; Sevik and Arli-Sokmen 2012; Nascimento et al. 2015; Thomas-Sharma et al. 2018). Direct economic losses results from the reduction in fruit weight caused by PhyRMV infections. However, the reduction in the number of fruits was the most important component.

The physiological quality of seeds can be assessed by germination testing, which, if planted under advantageous field conditions, provides maximum germination potential by enhancing seed performance after sowing (Jianhua and McDonald 1996; Lopes et al. 2010). The germination rate (90%) obtained from normal seedlings of healthy *P. peruviana* seeds in our study was lower than that reported by Lanna et al. (2013), who conducted biochemical oxygen demand chamber experiments and obtained 100% germination (using seeds from healthy plants). However, after evaluating three seed lots of *P. peruviana*, Diniz (2008) reported

Table 4 Vigor, primary root and primary shoot length of seedlings originated from seeds of healthy and PhyRMV-infected plants after accelerated aging

Treatment	Vigor (%)	Primary root length (mm)	Primary shoot length (mm)
48 h healthy	30 a	35.57 a	17.45 a
48 h PhyRMV-infected	33 a	37.50 a	16.55 a
CV (%)	30.49	22.70	18.50
48 h healthy with NaCl	25 a	33.50 a	16.32 a
48 h PhyRMV-infected with NaCl	31 a	36.75 a	15.92 a
CV (%)	37.85	21.86	23.47
72 h healthy	97 a	41.15 a	11.07 a
72 h PhyRMV-infected	76 b	36.75 b	12.85 a
CV (%)	9.97	26.70	16.06
72 h healthy with NaCl	51 a	41.17 a	12.8 a
72 h PhyRMV-infected with NaCl	53 a	33.07 b	12.2 a
CV (%)	22.53	23.06	22.24

CV, Coeficient of Variation. Means followed by the same letter did not differ by F-test at 5% probability

germination rates between 65% and 83% (also using seeds from healthy plants).

In addition, seed tolerance to stress was negatively affected by PhyRMV infection. Similar results were seen in cauliflower mosaic virus (CaMV) infection in *Arabidopsis thaliana* (Bueso et al. 2017). These authors suggested that changes in plant hormonal regulations caused by viral infection predisposing seeds to lower stress tolerance. Performing additional studies on seed quality and hormone regulation in healthy and PhyRMV-infected plants could better elucidate the influence of PhyRMV on plant hormones.

The current concept of seed vigor is: "the sum of all those properties which determine the potential for rapid, uniform emergence, and development of normal seedlings under a wide range of field conditions" (Baalbaki et al. 2009). The highest germination percentage occurred after an exposure period of 72 h at 41 °C. Several studies indicate that 72 h incubation at 41 °C for small seed species (TeKrony 1995; Panobianco and Marcos Filho 1998; 2001; Torres 2004; Lopes et al. 2010).

Some species of sobemoviruses are known to infect and be transmitted through seeds (Sõmera et al. 2015), but few studies have aimed to understand the effects of viral infection on seed quality. In sobemoviruses, results like this analysis were observed for *Sowbane mosaic virus* in *Chenopodium* spp., with average reductions of 6%, 15%, and 21% in germination for *C. quinoa*, *C. album*, and *C. murale*, respectively. Nevertheless, the virus did not affect seed viability for *C. album* and *C. murale*, suggesting that virus infection only influenced dormancy-breaking processes (Kazinczi et al. 2000). These findings are related to this study, where virus infection did not affect emergence speed index.

Although *P. peruviana* is currently cultivated at small scale, the economic impact on the production areas cannot be ignored. Host range tests showed that the virus is capable to infect other important solanaceous species, including *S. lycopersicum*, *C. annuum*, and *Nicotiana* spp. (Fariña et al. 2019), suggesting that in the future, it may cause significant economic impacts on these crops.

Authors' contributions Design of the study: FNS, EGS, AS. Conducting experiments: EGS, AS, MJG, CSM. Statistical analysis: EGS, AS. Data interpretation: FNS, EGS, AS, CMMS, CSM. Paper preparation: FNS, EGS, AS. Contributed reagents and materials: FNS, CMMS, DRB, AB, RTC. Critical paper review: FNS, EGS, AS, MJG, CSM, CMMS, DRB, AB, RTC. Language editing: FNS, ESG, AB. All authors discussed the results and contributed to the final manuscript.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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