SPROUTING RESPONSES OF *Solanum tuberosum* L. MINITUBERS TO HYDROGEN PEROXIDE AND SALICYLATE TREATMENT †

[RESPUESTAS DE BROTACIÓN DE *Solanum tuberosum* L. MINITUBÉRCULOS AL TRATAMIENTO CON PERÓXIDO DE HIDRÓGENO Y SALICILATOS]

Daimon Keller-Muñoz[1,2], Ricardo Martínez-Gutiérez[1], Martha E. Mora-Herrera[3], Flores-López R.[1] and Humberto A. López-Delgado[1*]

[1]Laboratorio de Fisiología-Biotecnología. Programa Nacional de Papa, Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP). Conjunto SEDAGRO. Metepec, Estado de México. C.P. 52140 México. Tel (722) 2 32 98 33, e-mail: lopez.humberto@inifap.gob.mx
[2]Centro de Biociencias. Universidad Autónoma de Chiapas. Carretera a Puerto Madero Km. 2.0 Tapachula; Chiapas, C.P. 30700 México.
[3]Centro Universitario Tenancingo Universidad Autónoma del Estado de México. Carretera Tenancingo-Villa Guerrero Km 1.5 Estado de México, C.P. 52400 México.
**Corresponding author*

SUMMARY

Background: Little is known about the long-term physiological effects of salicylic acid (SA) and hydrogen peroxide H_2O_2 on sprouting potato tubers and their possible short- and long-term effects as signaling molecules. **Objective:** To evaluate the effects of SA and H_2O_2 on the control of minituber sprouting. **Methodology:** The following research was carried out at the INIFAP facilities, Sitio Experimental Metepec, Edo. of Mexico. Microplants were transplanted into the soil in a greenhouse and sprayed twice a week with H_2O_2 (1, 5 mM) or SA (10^{-5}, 10^{-6} M), the number and fresh weight of minitubers per plant were evaluated. Subsequently, the minitubers were stored for sprouting, keeping half of each treatment at 8 °C and the other half at 18 °C. After 60 days of storage at 8 °C, the percentage, length and number of shoots per tuber were evaluated. **Results:** Low concentrations of H_2O_2 and SA significantly improved the sprouting percentage, while high concentrations significantly reduced it. Shoot length was reduced by 40% after treatment with 5 mM H_2O_2 and 10^{-6} M SA. After 60 days of storage at 18 °C, low concentrations of these molecules such as 1 mM H_2O_2 and 10^{-6} M SA reduced the sprouting percentage. The number of shoots per minituber increased by 10^{-5} M SA. **Implications:** This work demonstrated the potential of SA and H2O2 for practical application and tuber sprouting research. **Conclusion:** The results suggest that SA and H_2O_2 induce postharvest physiological effects on the sprouting of minitubers from the moment the plant is in cultivation.
Key words: long term effects; potato; storage; tuber dormancy.

RESUMEN

Antecedentes: Poco se sabe de los efectos fisiológicos a largo plazo del ácido salicílico (AS) y el peróxido de hidrogeno H_2O_2 en la brotación de tubérculos de papa y sus posibles efectos a corto y largo plazo como moléculas señalizadoras. **Objetivo:** Evaluar los efectos del AS y el H_2O_2 en el control de la brotación de minitubérculos. **Metodologia:** La siguiente investigación se realizó en las instalaciones del INIFAP, Sitio Experimental Metepec, Edo. de México. Microplantas se trasplantaron al suelo en un invernadero y se rociaron dos veces por semana con H_2O_2 (1, 5 mM) o AS (10^{-5}, 10^{-6} M) se evaluó número y peso fresco de tubérculos por planta. Posteriormente los minitubérculos se almacenaron para su brotación, manteniéndose la mitad de cada tratamiento a 8 °C y la otra mitad a 18 °C. Después de 60 días de almacenamiento a 8 °C se evaluó porcentaje, longitud y número de brotes por tuberculo. **Resultados:** Las bajas concentraciones de H_2O_2 y SA mejoraron significativamente el porcentaje de brotación, mientras que las

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ORCID-= Daimon Keller-Muñoz: https://orcid.org/0009-0009-7504-9750**; Ricardo Martínez-Gutiérrez**: https://orcid.org/0000-0003-4335-1065; **Martha Elena Mora-Herrera:** https://orcid.org/0000-0003-1362-7956; **Humberto Antonio López-Delgado:** https://orcid.org/0000-0002-1963-6362.

altas concentraciones lo redujeron significativamente. La longitud de los brotes se redujo en un 40 % después del tratamiento con 5 mM de H_2O_2 y 10^{-6} M de SA. Después de 60 días de almacenamiento a 18 °C, las bajas concentraciones de estas moléculas como 1 mM H_2O_2 y 10^{-6} M SA redujeron el porcentaje de brotación. El número de brotes por minitubérculo se incrementó en 10^{-5} M SA. **Implicaciones:** Este trabajo demostró el potencial del AS y el H2O2 para fines prácticos en controlar la brotación del tubérculo y para estudios fisiológicos de brotación de tubérculo. **Conclusión:** Los resultados sugieren que el AS y el H_2O_2 inducen efectos fisiológicos poscosecha sobre la brotación de los minitubérculos desde el momento en que la planta está en el cultivo.
Palabras clave: efectos a largo plazo; papa; almacenamiento; dormancia de tubérculo.

INTRODUCTION

Control of sprouting during potato tuber storage is challenging but important for different purposes, including fresh consumption, industrial processing and seed tuber production (Coleman and Coleman, 2000); however, sprouting causes quality loss through remobilization of starch and proteins, and shrinkage (Sonnewald, 2001; Börnke *et al*,. 2007).

Dormancy is the physiological state in which tubers do not sprout even under ideal physiological conditions for germination. This response depends on the genetic background, tuber development stage, and environmental and management conditions during tuber growth and storage (Aksenova *et al*., 2013; Sonnewald and Sonnewald, 2014; Muthoni *et al*., 2014; Mani and Hannachi, 2015). Dormancy is influenced by environmental and management conditions during growth and tuber storage (Mani *et al*., 2014). Temperature, water supply, soil fertility and the photoperiod during plant growth are all important environmental factors that regulate the sprouting response (Muthoni *et al*., 2014). In particular, temperature seems to have a major influence on sprouting (Turnbull and Hanke, 1985).

Dormancy of potato tubers during the postharvest period is called endodormancy (Lang *et al*., 1987) and involves an unknown endogenous signal that mediates the inhibition of meristem growth (Suttle, 2004b).

After a transition period of 1-15 weeks, depending on the storage conditions and variety, dormancy is broken and apical buds start to grow (Wiltshire and Cobb, 1996). Farmers sometimes need to promote or retard sprouting depending on the time of year (Johansen *et al*., 2008; Salimi *et al*., 2010).

The breaking of dormancy and the beginning of sprout growth in the tuber involve complex hormonal changes, many of which alter the nutritional quality of the potato (Suttle, 2004a). Several commercial compounds to break the dormancy of tubers have been tested such as thiourea, carbon disulfide, ethylene chlorohydrin, and rindite (Bryan, 1989; Rehman *et al*., 2003) however, most of them are extremely volatile, very dangerous, corrosive and must be handled with extreme care. Additionally, the application of some chemical agents raises environmental and consumer concerns (Muthoni *et al*., 2014).

It was suggested that catalase (CAT) and H_2O_2 mediate tuber sprouting (Bajji *et al*., 2007) and that CAT activity can be regulated by salicylic acid (SA), modifying the H_2O_2 content in potato plants (Mora-Herrera et al. 2005; Mora-Herrera and López-Delgado, 2006). Also, both SA and H_2O_2 induce growth retardation in *in vitro* potato plants (López-Delgado and Scott, 1997; López-Delgado *et al*., 1998a, López-Delgado *et al*., 1998b) and can have long-term effects on potato physiology (Sánchez-Rojo *et al*., 2011; López-Delgado *et al*., 2012; Aguilar-Camacho *et. al*., 2016; López-Delgado *et al*., 2018).

Information about the long term physiological effects of SA and H_2O_2 on potato tuber sprouting is scarse. Bearing in mind the physiological effects of H_2O_2 and SA on potato growth and the long-term effects on potato physiology, we reasoned that these signal molecules could mediate tuber sprouting in the short and long term. The aim of this research was to evaluate the potential effects of SA and H_2O_2 on tuber sprouting in the long term at two storage temperatures.

MATERIALS AND METHODS

Plant material and culture conditions

Virus-free *Solanum tuberosum* L. microplants of clone 040138 from the *in vitro* Germplasm Bank of the National Institute for Agriculture and Livestock Research (INIFAP) were used for experiments in Metepec, México. Axillary buds were subcultured in jars on MS propagation medium (Murashige and Skoog, 1962) every 30 d and grown at 18±1 °C with a 16-h photoperiod (fluorescent lights, 35 µmol m^{-2} s^{-1}, 400-700 nm) to keep a microplant stock.

Greenhouse treatments

Thirty-day-old microplants were transplanted to pots (32 × 12 cm) containing peat-moss and perlite. The plants were cultured for 100 days after transplanting (DAT) and each pot was allocated to an experimental unit, with 40 plants per treatment (one plant/pot). The experiments were performed three times. The plants were fertilized every 15 days and watered once a week.

Plants were fertilized (170 N, 230 P, 170 K, 90 S, 20 Ca, 20 Mg) every fifteen days and watered (soil holding waters capacity) twice a week. Plants were sprayed twice a week (30-80 DAT) with 1 or 5 mM H_2O_2 or 10^{-5} or 10^{-6} M SA, or water (control) at pH 5.6 (10 mL/plant) in randomized arrays. Harvesting was performed at 100 DAT.

Minituber storage

Fifty minitubers harvested from each treatment and the control were distributed into two groups.

Minitubers (20-30 mm diameter) of both groups were placed under diffuse light (Walker and Fuglie, 2005) at two temperatures for sprouting, with half (25 minitubers/treatment) at 8 °C and half (25 minitubers/treatment) at 18 °C. The percentage of sprouted minitubers, minituber fresh weight, number of sprouts/minituber and sprout length were recorded after 60 and 100 d of storage. A minituber with one sprout at least 3 mm length was considered a sprouted minituber. All the sprouts on a minituber were quantified to evaluate the sprout number. Sprout length was estimated considering only the longest sprout on each minituber bearing in mind that it was the first sprout developed with the principal growth of the tuber (Bajji *et al.*, 2007; Hosseini *et al*., 2011).

Statistical Analysis

The data were tested for differences between treatments using one-way analysis of variance (ANOVA) and Duncan's multiple range test (Duncan, 1955), and scored as significant if $P < 0.05$ using the SAS software. A completely randomized design was used with two factors, the doses of each compound, and the storage temperatures. The means and standard errors (mean ± SE) were recorded.

RESULTS

Harvest

The fresh weight of the minitubers was significantly ($P < 0.05$) increased by SA and H_2O_2, especially 1 mM H_2O_2 and 10^{-5} M SA, which significantly ($P < 0.05$) increased the fresh weight by 96 % and 1.03-fold, respectively, compared with the control. The number of minitubers was significantly ($P < 0.05$) increased by 30 % in 1 mM H_2O_2 treatment (Table 1).

Sprouting

60 days of storage

The 8 °C treatment induced both a reduction and an increase in the sprouting percentage. Low concentrations of H_2O_2 and SA significantly ($P < 0.05$) increased the sprouting percentage, whereas high concentrations significantly ($P < 0.05$) reduced it (Fig. 1). No significant differences were observed in the sprouts number/minituber at 8 °C or 18 °C (data not shown).

At the same temperature 5 mM H_2O_2 and 10^{-6} M SA treatments both significantly ($P < 0.05$) reduced the sprout length by 40.0 % compared with the control (Fig. 2).

At 18 °C, the sprouting percentage was significantly ($P < 0.05$) decreased compared with the control under low concentrations of H_2O_2 and SA (Fig. 3).

100 days of storage

No significant differences were observed in the sprouting percentage at 18 °C (data not shown). The number of sprouts per minituber was increased significantly ($P < 0.05$) by 10^{-5} M SA compared with the control (Fig. 4).

Table 1 Fresh weight and minitubers number. Minitubers were harvested from sprayed plants with SA and H_2O_2. Experiments were performed three times (n=40 plants/treatment). Data are means ± SE. Different letters differ significantly by ANOVA and Duncan test (P <0.05).

Treatments	Minituber fresh weight (g/planta)	Minitubers number/plant
Control	$6.56 \pm 0.64^{c\dagger}$	5.00 ± 0.53^{b}
1 mM H_2O_2	12.92 ± 0.73^{a}	6.50 ± 0.52^{a}
5 mM H_2O_2	10.43 ± 0.74^{b}	4.90 ± 0.48^{b}
10^{-6} M SA	12.04 ± 0.54^{ab}	6.10 ± 0.42^{ab}
10^{-5} M SA	13.34 ± 0.73^{a}	5.55 ± 0.40^{ab}

SA= Salicylic acid. H_2O_2= Hydrogen peroxide.

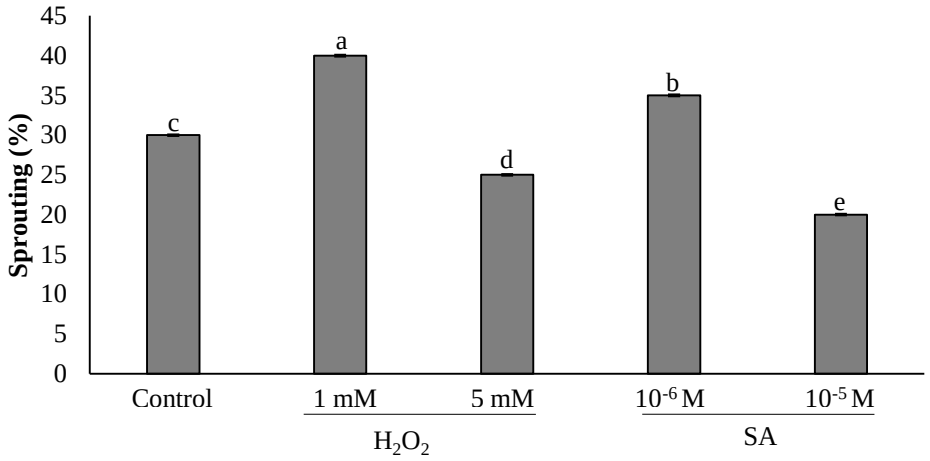

Figure 1. Percentage of sprouted minitubers harvested from sprayed plants after 60 d of storage at 8 °C. Experiments were performed three times (n=75). SA= Salicylic acid, H_2O_2= Hydrogen peroxide. Data are means ± SE. Bars labeled with different letters differ significantly by ANOVA and Duncan test (P <0.05).

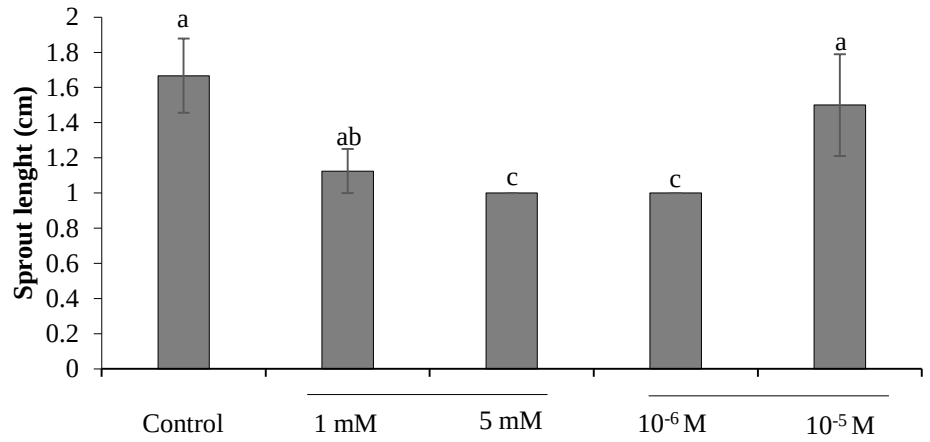

Figure 2. Sprout length of sprouted minitubers harvested from sprayed plants after 60 d of storage at 8 °C. Experiments were performed three times (n=75). SA= Salicylic acid, H_2O_2= Hydrogen peroxide. Data are means ± SE. Bars labeled with different letters differ significantly by ANOVA and Duncan test (P <0.05).

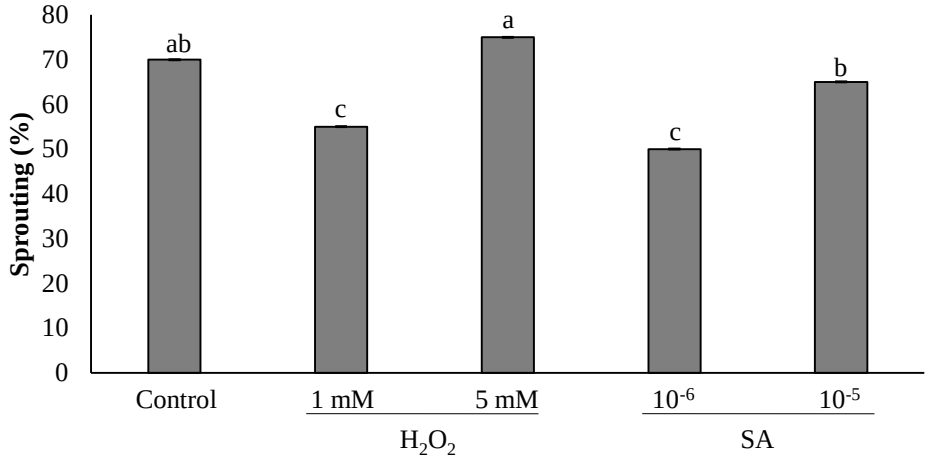

Figure 3. Percentage of sprouted minitubers harvested from sprayed plants after 60 d of storage at 18 °C. Experiments were performed three times (n=75). SA= Salicylic acid, H_2O_2= Hydrogen peroxide. Data are means ± SE. Bars labeled with different letters differ significantly by ANOVA and Duncan test (P <0.05).

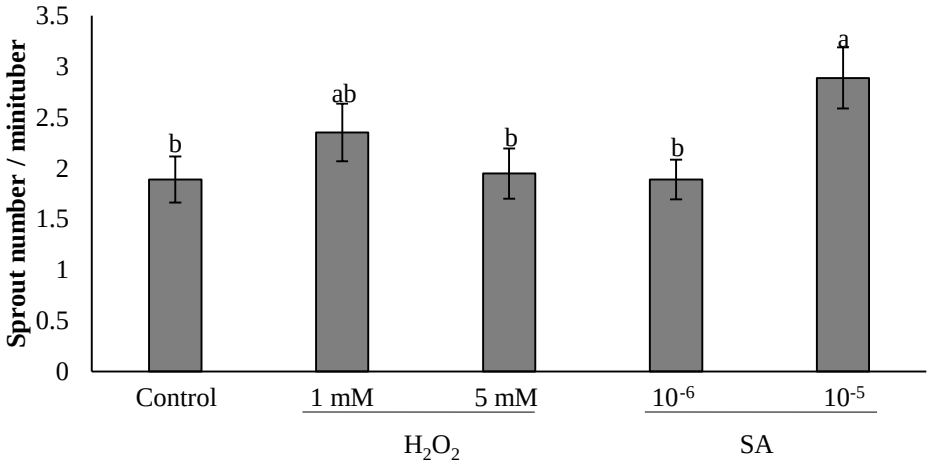

Figure 4. Number of sprouts per minituber harvested from sprayed plants after 100 d of storage at 18 °C. Experiments were performed three times (n=75). SA= Salicylic acid, H_2O_2= Hydrogen peroxide. Data are means ± SE. Bars labeled with different letters differ significantly by ANOVA and Duncan test (P <0.05).

DISCUSSION

Potato tuber dormancy is affected by genotype, physical or chemical stress, and pre- and post-harvest conditions (Sonnewald, 2001; Suttle, 2004b; Mani and Hannachi, 2015). This work demonstrates the long-term effects of SA and H_2O_2 on tuber sprouting and temperature mediation of these responses. The results demonstrated that spraying plants with SA and H_2O_2 affected microtuber postharvest physiology. The effects of these treatments on the sprouting percentage, and length and number of sprouts were observed after storage. Spraying H_2O_2 and SA on potato plants grown in a greenhouse significantly ($P < 0.05$) increased the fresh weight of minitubers; moreover, H_2O_2 significantly ($P < 0.05$) increased the number of minitubers at the lowest concentration tested (1 mM, Table 1). These results agree with previous reports where H_2O_2 (Romero-Romero and López-Delgado, 2009) and SA (Sánchez-Rojo *et al*., 2011) significantly increased the number and weight of minitubers in plants infected by phytoplasma. The potential effect of H_2O_2 on minituber weight observed in this work was also reported in microtubers under the same H_2O_2 concentrations (López-Delgado *et al*., 2012). These results could be associated with responses to biotic and abiotic stress mediated by SA and H_2O_2 under stress conditions (Romero-Romero and López-Delgado, 2009).

Studies have shown that hydrogen peroxide regulates ethylene, jasmonic acid and SA synthesis, which removes dormancy (Kwak *et al*., 2006). Previous reports demonstrated that oxidative stress, specifically H_2O_2, induces dormancy release (Bajji *et al*., 2007). It has been reported that H_2O_2 not only induces *in vitro* tuberization but also significantly enhances the sprouting of microtubers kept at 20 °C (López-Delgado *et al*., 2012). In this work, physiological effects of H_2O_2 on tuber sprouting were demonstrated, these signaling effects of H_2O_2 could be mediated by CAT activity, the antioxidant enzyme which in the first place scavenge H_2O_2. It was demonstrated that treating dormant potato tubers with thiourea (a chemical CAT inhibitor) broke dormancy and accelerated sprouting (Bajji *et al*., 2007). Repression of CAT activity accelerated potato tuber germination and was associated with H_2O_2 accumulation (M´Hamdi *et al.*, 2014). Different responses of CAT activity to the effects of H_2O_2 have been observed in potato plants under different culture conditions, such as in plants infected by phytoplasma under greenhouse conditions (Martínez-Gutiérrez *et al*., 2012) and *in vitro* plants (Mora-Herrera *et al*., 2005).

The literature documents a complex relationship between SA and H_2O_2 signaling in plants; SA can increase H_2O_2 (Dat *et al.*, 2000) and can also be induced by H_2O_2 (Chamnongpol *et al*., 1996). SA has been reported as a CAT inhibitor in potato (López-Delgado *et al*., 1998b; Mora-Herrera *et al.*, 2005). The sprouting responses induced by these molecules in this work might be related to the mechanism suggested by M´Hamdi *et al*., (2014), where inactivation of CAT leads to increased ascorbate peroxidase activity, and these changes activate the glutathione cycle and pentose phosphate pathway, and subsequently release dormancy. The long term effects of spraying plants with these molecules on CAT activity and H_2O_2 content in tubers are worthy of further investigation.

Temperature seems to have a major influence on tuber sprouting (Turnbull and Hanke, 1985; Mani and Hannachi, 2015), and is also one of the most important physical factors determining the length of the dormancy period during storage.

Hartmans and Van Loon, (1987) reported that temperatures over 12 °C affected the capacity and vigor of sprouts compared with tubers stored at 4 °C, intensifying respiration, reactive oxygen species levels such as internal H_2O_2 in tubers, and antioxidant enzymes like CAT. It was suggested that dormancy length is inversely proportional to temperature (Wiltshire and Cobb, 1996). However, the sprouting capacity of tubers can increase with increasing temperature (Ridwan *et al*., 2014). Interestingly, inverse effects were observed after 60 days of storage in tubers depending on the temperature; at 8 °C, the low concentrations of H_2O_2 (1 mM) and SA (10^{-6} M) significantly ($P < 0.05$) enhanced the sprouting percentage (Fig. 1), whereas at 18 °C, the same concentrations significantly ($P < 0.05$) reduced it (Fig. 3). These results confirm the long-term effects of spraying plants with these molecules on tuber sprouting. Sprout length was decreased at 8 °C by 5 mM H_2O_2 and 10^{-6} M SA after 60 d of storage (Fig. 2). The effects observed on sprout length agree with previous reports where salicylate (López-Delgado *et al*., 1998a) and H_2O_2 (López-Delgado *et al*., 1998b) induced growth retardation in *in vitro* potato plants, associated with antioxidant activity, such as catalase.

The practical utility of SA and H_2O_2 treatments as demonstrated in the present study is strong justification for continued investigation of the physiological role of these signal molecules in the control of tuber sprouting during storage. Additionally, their application raises no environmental or consumer concerns because they are ecologically innocuous.

CONCLUSION

Responses such as the sprouting percentage, sprout length and number of sprouts/minituber in potato, can be affected in the long term by SA and H_2O_2 from the time when the plant is in the growing phase, and are mediated by storage temperature. These results suggest that SA and H_2O_2 induce postharvest physiological effects on minituber sprouting. These physiological responses could be important for practical application, mediating the number of stems of the plant, since this is linked to the sprouting percentage and the number of sprouts/minituber. Tuber yield is related with the number of stems of the plant.

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Compliance with ethical standards. The work does not require approval by a (bio)ethical committee.

Data availability. Data is available within the paper. Additional information can be obtained from the corresponding author.

Author contribution statement (CRediT). D. Keller-Muñoz, writing original, draft and methodology, writing-review, editing validation and data curation**. R. Martínez-Gutiérez,** writing-review and editing, methodology, advise. **M. E. Mora-Herrera**, writing-review and editing, methodology. **R. Flores-López,** writing-review and editing. **H. A. López-Delgado**, conceptualization, writing-review and editing, funding acquisition, supervision and validation.

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