

# Seed dormancy and germination in tree tomato (*Solanum betaceum* Cav.) and lulo (*Solanum quitoense* Lam.)

Latencia y germinación de semillas de tomate de árbol (*Solanum betaceum* Cav.) y lulo (*Solanum quitoense* Lam.)



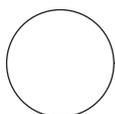
ALBA MARINA TORRES-GONZÁLEZ<sup>1,2</sup>

**Lulo and tree tomato fruits.**

Photo: A.M. Torres-González

## ABSTRACT

Tree tomato (*Solanum betaceum* Cav.) and lulo (*Solanum quitoense* Lam.) fruits enjoy high consumption and commercialization in Colombia. Seed dormancy has been reported for both species, and their propagation depends on seeds. The optimal germination conditions for these species are not well known. Thus, the temperature regimes for the seed germination were based on the mean, minimum and maximum temperatures of the locations where the crops were grown. Germination tests were carried out in four replicates of 50 seeds each on Petri dishes for both crops. Six temperature conditions and four pre-treatments were evaluated to break the seed dormancy for several seed lots. *S. betaceum* and *S. quitoense* exhibited shallow seed dormancy, and less dormancy was detected in the commercialized cultivars, such as *S. betaceum* cv. Tamarillo and *S. quitoense* (*i.e.* common lulo). For both species, the most recently harvested seeds had more germination capacity than the seeds stored for several months at a low seed moisture content (4%) and low storage temperature (20°C). The seed dormancy of *S. betaceum* and *S. quitoense* was broken successfully by applying GA<sub>3</sub> (2,000 mg L<sup>-1</sup>) or alternating temperatures (*e.g.* 25/15°C). However, both treatments at the same time did not provide an additional benefit to promote seed germination. Potassium nitrate (1%) promoted seed germination in the *S. betaceum* seeds at both constant and alternating temperatures and in the *S. quitoense* seeds, only when alternating temperatures were applied. The application of GA<sub>3</sub> increased the rate of germination more than KNO<sub>3</sub> for both species at all temperatures. Using any of these treatments would work well to break seed dormancy in *S. betaceum* and *S. quitoense*, and the most convenient option could be selected depending upon budget and other resources.



**Additional key words:** gibberellic acid; potassium nitrate; seed storage; plant propagation.

<sup>1</sup> Universidad del Valle, Faculty of Sciences, Department of Biology, Cali (Colombia). ORCID: Torres-González, A.M.: 0000-0002-3010-2505

<sup>2</sup> Corresponding author. [alba.torres@correounivalle.edu.co](mailto:alba.torres@correounivalle.edu.co)

## RESUMEN

Tomate de árbol (*Solanum betaceum* Cav.) y lulo (*Solanum quitoense* Lam.) son frutas altamente consumidas y comercializadas en Colombia. Latencia de semillas ha sido reportada para ambas especies y su propagación se realiza por semillas. Las condiciones óptimas de germinación no son bien conocidas para estas especies. Así, los regímenes de temperatura para la germinación de las semillas fueron usados con base en la temperatura media, mínima y máxima de las localidades donde crecen estos cultivos. Se realizaron pruebas de germinación en cajas de Petri, con seis temperaturas y cuatro pre-tratamientos que fueron probados para romper la latencia de varios lotes de semillas. Los resultados muestran que las dos especies tienen latencia, en menor medida en los cultivares más comercializados, *S. betaceum* cv. Tamarillo y *S. quitoense* (i.e. cultivar común). Para ambas especies, las semillas recién cosechadas tuvieron mayor promoción de la germinación que las almacenadas por varios meses con bajo contenido de humedad de la semilla (4%) y baja temperatura de almacenamiento (20°C). La latencia de las semillas de *S. betaceum* y *S. quitoense* se rompió exitosamente con la aplicación de GA<sub>3</sub> (2,000 mg L<sup>-1</sup>) o temperaturas alternadas (e.g. 25/15°C). Ambos tratamientos al mismo tiempo no tuvieron un beneficio adicional para promover la germinación. KNO<sub>3</sub> (1%) promovió la germinación de semillas de *S. betaceum* a temperaturas constantes y alternadas, y de semillas de *S. quitoense* solamente a temperaturas alternadas. El pre-tratamiento con GA<sub>3</sub> incrementó la velocidad de germinación más que KNO<sub>3</sub>, para ambas especies y en todas las temperaturas. Se sugiere usar cualquiera de estos tratamientos que funciona bien para romper la latencia de semillas de *S. betaceum* and *S. quitoense*, y la opción más conveniente puede ser seleccionada dependiendo del presupuesto y otros recursos.

**Palabras clave adicionales:** ácido giberélico; nitrato de potasio; almacenamiento de semillas; propagación vegetal.

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## INTRODUCTION

Solanaceae is one of the main plant families of economic importance in Colombia because it provides several food species. Among the edible Solanaceae species, tree tomato (*Solanum betaceum* Cav. = *Cyphomandra betaceum* (Cav.) Sendtn.) and lulo (*Solanum quitoense* Lam.) fruits enjoy high consumption and commercialization in Colombia. Despite being cultivated species, the germplasm of both species studied with COSII molecular markers have a high population structure, which could be the result of low genetic migration between planted populations (Enciso-Rodríguez *et al.*, 2010).

*S. betaceum* is a domesticated species grown throughout the Andes between 600 and 3,200 m a.s.l. (Bohs, 2015). Moreover, *S. betaceum* is grown for commercial purposes in New Zealand with the name “Tamarillo”, in the Mediterranean area and in Germany (Samuels, 2015). Thus, the name “Tamarillo” has become the standard commercial designation for *S. betaceum* in Europe, which includes fruits with a dark-purple and red skin that have purple pulp and fruits with a yellow and orange skin with yellow pulp (The Climbing Fig, 2020). However, in the domestic market of

Colombia, the name “Tamarillo” is used exclusively for fruits with a purple skin and pulp.

*S. quitoense* is cultivated most commonly in Colombia, Ecuador, and Peru at altitudes between 800 and 2,000 m a.s.l. (Bohs, 2015; Gallo *et al.*, 2018). In Colombia, the number of lulo crops has grown because domestic demand has increased (Arias and Rendon, 2015). Two varieties of *S. quitoense* commercially cultivated are *S. quitoense* var. *septentrionale* with spines and *S. quitoense* var. *quitoense* without spines (Samuels, 2015). *S. quitoense* is considered one of the species with high gastronomic innovation in the Andean biodiversity (Corzo-Barragan *et al.*, 2016) and is known as the “golden fruit of the Andes” (Ramirez *et al.*, 2018). There is an interspecific hybrid between *S. quitoense* and *S. hirtum* known as *S. quitoense* cv. “La Selva”, which exhibited greater genetic variability than *S. quitoense* (Fory *et al.* 2010).

*S. quitoense* is propagated by seeds to obtain more vigorous plants, but *S. quitoense* “La Selva” has to be propagated asexually by cuttings or *in vitro* micropropagation to conserve the hybrid characteristics (Franco

*et al.*, 2002). The propagation of these *Solanum* fruit crops depends mainly on seeds. Micro propagation of hypocotyls, which is an efficient option for massive propagation of *S. betaceum*, starts with seed germination (Criollo *et al.*, 2016). However, seeds frequently exhibit dormancy as an evolutive response of the species to prevent germination until the appropriate time (Shut *et al.*, 2016).

Seed dormancy is found in several cultivated species of *Solanum*. For instance, seed germination of the common tomato (*Solanum lycopersicum* L. = *Lycopersicon esculentum* Mill.) is restricted by seed tissues, such as the embryo by controlling the water potential, the endosperm by controlling cell wall hydrolysis, and the testa by preventing radicle protrusion (Hilhorst, 1997). In tomatoes, cell cycle activity before germination is required, accompanied by nuclear DNA replication, but is blocked in dormant and gibberellin-deficient tomato seeds (Groot *et al.*, 1997). The weed species *Solanum nigrum* and *S. physalifolium* exhibit variation in the level of dormancy, enabling populations to escape from weed control or extreme climatic conditions (Taab and Andersson, 2009).

Germination in Solanaceae species is frequently light sensitive. In tobacco (*Nicotiana tabacum*), there is light dependence during seed germination (Koo *et al.*, 2015), but *Solanum elaeagnifolium* has similar germination in dark or light conditions (Stanton *et al.*, 2012).

Gibberellic acid promotes germination successfully in potato (*Solanum tuberosum*) seeds when it is applied at high concentrations of 2,000 mg L<sup>-1</sup> and pre-applied for 24 h (Spicer and Dionne, 1961). In *S. betaceum*, alternating temperatures of 28/24°C for 12/12 h with applications of GA<sub>3</sub> (1,000 mg L<sup>-1</sup>) promoted seed germination, but with an application of KNO<sub>3</sub> (0.2%), the seed germination of *S. betaceum* and *S. quitoense* decreased (Cárdenas *et al.*, 2004).

Breaking seed dormancy is particularly important for agricultural production because seed germination is the initial phase that ensures the establishment of seedlings and, finally, the crop yield. Thus, this research answered the questions: 1) Is it possible to promote seed germination of *S. betaceum* and *S. quitoense* by applying chemical treatments and incubating at constant or alternate temperatures? 2) Are there differences in seed dormancy between cultivars of *S. betaceum* and *S. quitoense*?

## MATERIALS AND METHODS

### Plant material

Mature *S. betaceum* and *S. quitoense* fruits were purchased from local markets in Cali, Colombia. The storage condition of the seeds are provided in Tab. 1. The seed extraction and conditioning were done following the protocol to extract seeds from fleshy fruits (Torres-González, 2018). All seeds were dehydrated, and some seed lots were stored in cold conditions to prevent loss of viability before testing (Hong and Ellis, 1996). The moisture content test of the seed lots was determined before the germination tests according to the high-constant-temperature-oven method, namely 1 h drying at 130°C (ISTA, 2016). Two samples of 1-2 g each of the entire seeds were dried in Pyrex Petri dishes (85×15 mm) in an oven (Thermocenter, SalvisLab, Switzerland) and weighed on an analytical balance (Metler Toledo International Inc., Switzerland) to the nearest 0.01 mg before and after drying. The moisture content was calculated as percentage wet basis (ISTA, 2016).

### Germination tests

Each germination test consisted of four replicates of 50 seeds. No fungicides were added to the substrate to avoid extra chemical factors affecting germination. Scarification for the seeds of these species was not needed.

Constant illumination and alternating temperature incubators were used for the germination tests. The thermoperiod was set for 16/8 h at alternating temperatures. In each case, the first temperature listed for each alternating-temperature regime was provided for 16 h of each daily cycle; *e.g.* 15/25 indicates 15°C applied for 16 h d<sup>-1</sup> and 25°C applied for 8 h d<sup>-1</sup>. The temperature regimes were based on the mean, minimum and maximum temperatures of the locations where the crops were grown, according to Vargas-Figueroa and Torres-González (2018). The photoperiod was provided for 16 h per day for both constant and alternating temperatures. In the latter case, the lighting period was synchronous with the longer thermoperiod.

Germination was recorded as radicle protrusion ( $\geq 2$  mm length). The tests were carried out on 8.5 x 20 mm Petri dishes with two filter papers (Whatman

**Table 1. Storage time, temperature and moisture of *Solanum betaceum* and *S. quitoense* seeds.**

Cultivar	Seed lot	Time (months)	Temperature (°C)	Moisture(%)
<i>S. betaceum</i> cv. Tamarillo	A	7	20	4.0
<i>S. betaceum</i> cv. Tamarillo	B	0	-	4.0
<i>S. betaceum</i>	C	7	20	4.0
<i>S. betaceum</i>	D	0	-	4.0
<i>S. quitoense</i>	A	2	20	4.0
<i>S. quitoense</i> cv. La Selva	B	0	-	4.0

Ltd., grade 181) moistened with 4.5 mL of deionized water. One Petri dish was used for each replicate, and four dishes were placed in a loosely folded plastic bag. The duration of the test was 21 d. The germination tests were checked three times a week to record the progress of germination during tests.

Several chemical pre-treatments were applied for 24 h at 20°C before beginning germination tests; 30 mL of solution was used to soak 100-200 seeds.

### Experiment design

For each species, the seed lots included the varieties cultivated and commercialized in Colombia (Tab. 1). The temperature regimes were 1) constant temperature, 15°C; 2) constant temperature, 25°C; 3) alternating temperatures, 15/25°C; 4) alternating temperatures, 25/15°C, 5) alternating temperatures, 20/30 °C; and 6) alternating temperatures 20/35°C. The controls and treatments were: 1) dry seeds, as dry control; 2) deionized water, as pre-applied control; 3) gibberellic acid (GA<sub>3</sub>), 2,000 mg L<sup>-1</sup>; and 4) potassium nitrate (KNO<sub>3</sub>), 1%.

The experiments had a factorial design that differed among the species. Thus, for *S. betaceum* the factorial was 4×6×4, and, for *S. quitoense*, it was 2×6×4, indicating the number of seed lots, temperature regimes and pre-treatments applied, respectively.

### Statistical analysis

The rate of germination was calculated with the formula used by Torres-González (2018):  $R = \sum (n / (d * n))$ , where  $n$  is the number of seeds germinated on day  $d$ , and,  $d$  is the number of days from the beginning of the germination test.

For normality of variances for the analysis of variance, the germination percent was transformed to

angles using the arcsine function for the formula: angles (radians) =  $\text{Arcsin}\sqrt{(\% \text{ germination}/100)}$ . The angles were transformed from radians to degrees. The analysis of variance (ANOVA) was used to compare the variation between factors. An analysis of normality and homogeneity of variance of the transformed data was performed. The SAS software was used for these analyses (SAS, 2020). The  $\alpha$  level to determine the significance in the F test was 0.05. When no interaction between factors was found, *a posteriori* Tukey test was applied ( $P \leq 0.05$ ).

## RESULTS

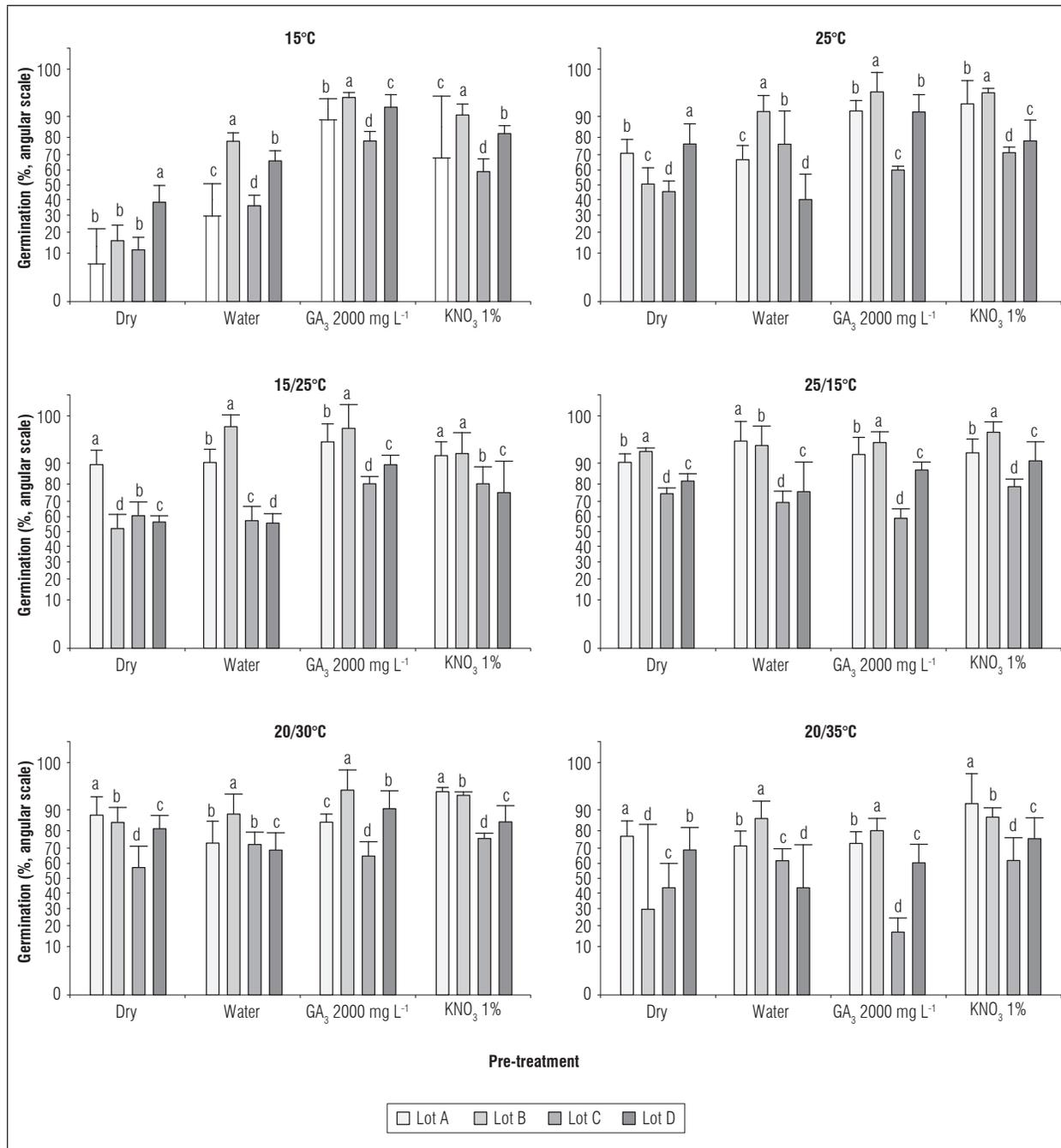
### *Solanum betaceum* Cav. (tree tomato)

Depending upon the treatment combination, the germination ranged from 13 to 99% (Fig. 1,  $P < 0.05$ ). Seed lots A and B of cultivar Tamarillo had higher germination than the common cultivar (lots C and D). In the majority of treatments for both cultivars, the recently extracted seeds (lots B and D) germinated better than the seeds stored for seven months (lots A and C). The alternating temperatures 25/15°C gave the greatest germination for all treatments over the other temperature regimes. The interaction between the effect of alternating temperature (25/15°C) and application of either gibberellic acid or potassium nitrate for seed lot B showed that the two different pre-treatments not only had similar effects but also had a similar effect to that of temperature alternations, while there were no additive effects from pre-treatment and alternation (Fig. 2).

In consequence, high germination was obtained with gibberellic acid and potassium nitrate pre-treatment at constant temperature (97 and 95%, respectively) or in the water control at an alternating temperature of 25/15°C (95%). The lowest germination occurred

for dry seeds at a constant temperature of 15°C for all seed lots (13-40%), demonstrating that soaking in water at this temperature was beneficial (38-80%), (Fig. 1).

The rate of germination was affected by all factors with significant interactions between them ( $P \leq 0.05$ ). The highest rate of germination was at 25 and 25/15°C with pre-treatment in gibberellic acid



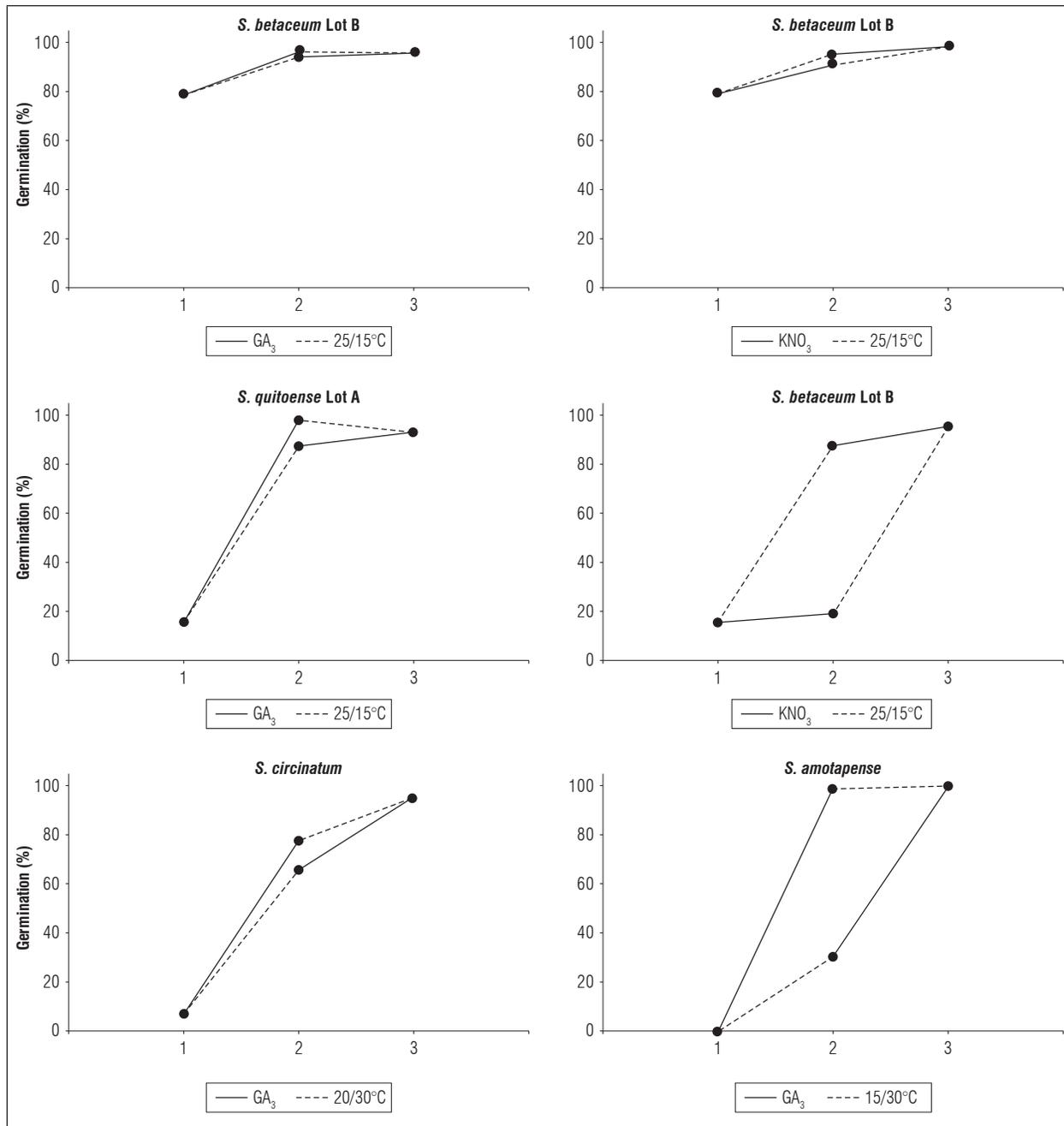
**Figure 1. Effect of constant or alternating temperature and several pre-treatments on the germination of four seed lots of *Solanum betaceum* Cav. Lot A: cv. Tamarillo, 7 months in storage, lot B: cv. Tamarillo, 0 months in storage, lot C: common tree tomato, 7 months in storage, lot D: common tree tomato, 0 months in storage. Means with different letters indicate significant statistical difference within each pre-treatment according to the Tukey test ( $P \leq 0.05$ ;  $n=4$ ). The vertical bars indicate  $\pm$  standard error.**

(Fig. 3). In these regimes, lots A, B and D showed similar rapid rates of germination, with lot C being appreciably slower.

### *Solanum quitoense* (lulo)

The germination was affected by all factors, their second-order interaction and by the first-order

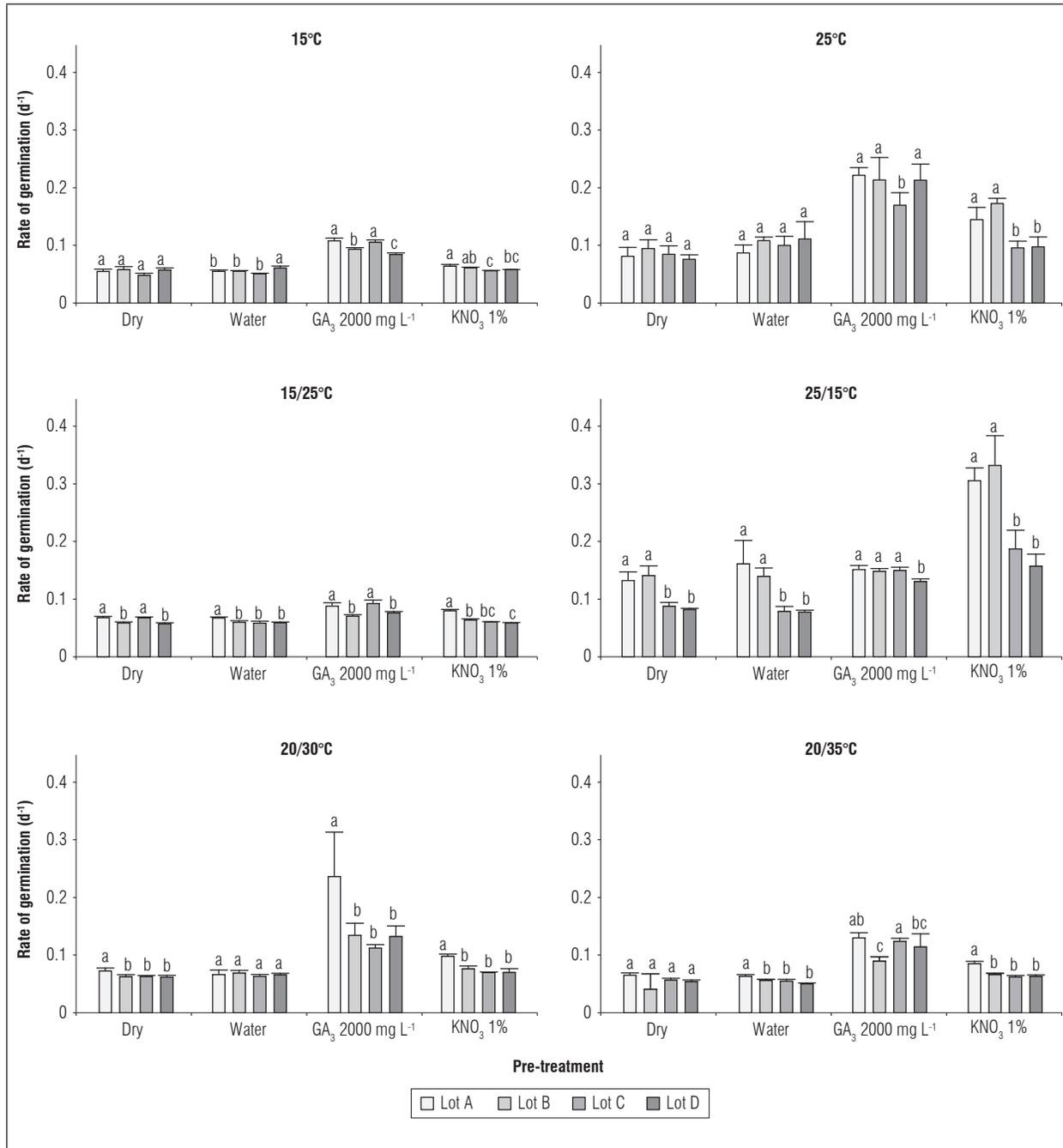
interaction between temperature and pre-treatment ( $P \leq 0.05$ ). Generally, lot A (*i.e.* common cultivar) had greater germination in the tested temperatures and treatments than lot B (cv. La Selva), (Fig. 4). The alternating temperature regime 25/15°C gave a higher germination for all treatments, even for the dry and water controls. However, gibberellic acid promoted



**Figure 2.** Interaction between factors promoting germination of *Solanum betaceum* Cav. Lot B (control: 15°C, water) and *S. quitoense* Lam. Lot A (control: 15°C, water). 0: no factors applied, 1: one factor applied, 2: two factors applied.

germination substantially at temperatures with less promotion of seed germination (e.g. 91-100% at 25°C). The interaction between gibberellic acid and alternating temperature (25/15°C) was, therefore,

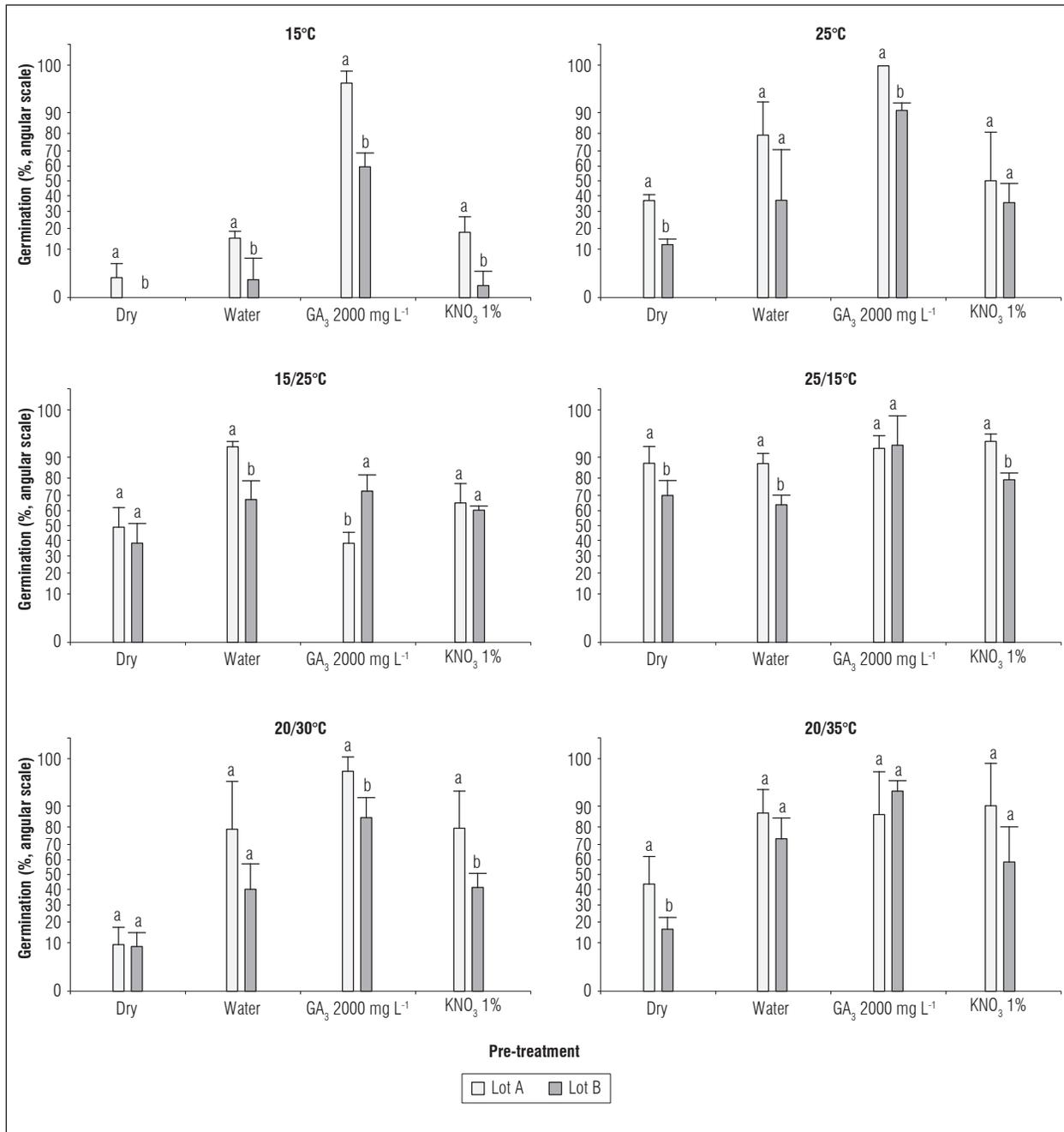
negative because either factor promoted close to full germination (Fig. 2). In contrast, the effects of alternating temperature (25/15°C) and pre-treatment with potassium nitrate were additives (Fig. 2).



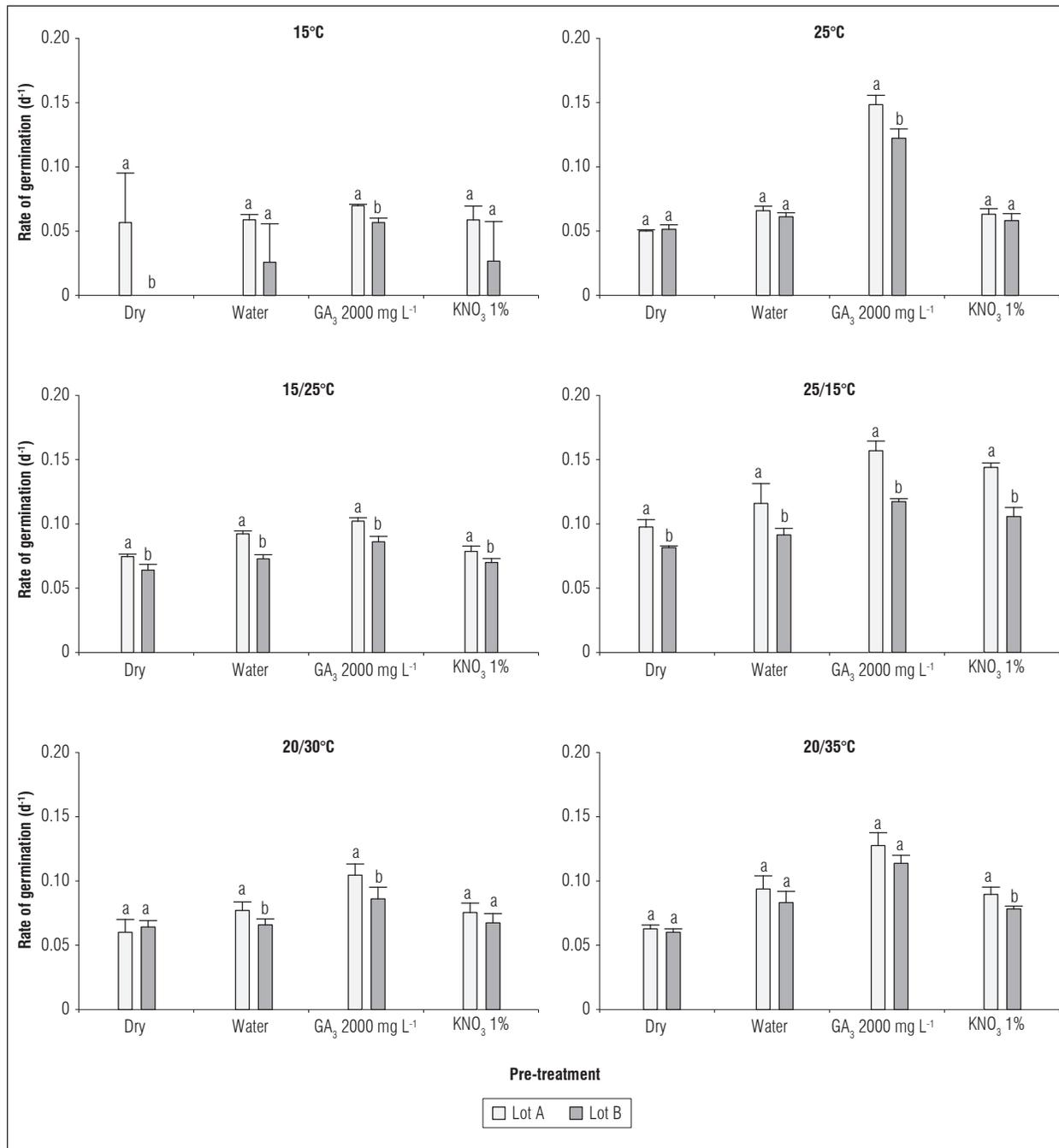
**Figure 3. Effect of constant or alternating temperature and pre-treatment on the rate of germination of four seed lots of *Solanum betaceum* Cav. Lot A: cv. Tamarillo, 7 months in storage, lot B: cv. Tamarillo, 0 months in storage, lot C: common tree tomato, 7 months in storage, lot D: common tree tomato, 0 months in storage. Means with different letters indicate significant statistical difference within each pre-treatment according to the Tukey test ( $P \leq 0.05$ ;  $n=4$ ). The vertical bars indicate  $\pm$  standard error.**

The rate of germination was significantly affected by all factors and most of their interactions ( $P \leq 0.05$ ). The highest rate of germination was found for the common variety (lot A) at 25/15°C (16/8h) with

pre-treatment in  $GA_3$  (Fig. 5). In all temperature regimes, pre-treatment with  $GA_3$  provided the most rapid germination.



**Figure 4.** Effect of constant or alternating temperature and several pre-treatments on the germination of two seed lots of *Solanum quitoense* Lam. (21 d duration), Lot A: common lulo, 2 months in storage, Lot B: cv. La Selva, 0 months in storage. Means with different letters indicate significant statistical difference within each pre-treatment according to the Tukey test ( $P \leq 0.05$ ;  $n=4$ ). The vertical bars indicate  $\pm$  standard error.



**Figure 5. Effect of constant or alternating temperature and several pre-treatments on the rate of germination of two seed lots of *Solanum quitoense* Lam. Lot A: common lulo, 2 months in storage, Lot B: cv. La Selva, 0 months in storage. Means with different letters indicate significant statistical difference within each pre-treatment according to the Tukey test ( $P \leq 0.05$ ;  $n=4$ ). The vertical bars indicate  $\pm$  standard error.**

## DISCUSSION

The germination varied considerably among the seed lots, the different temperature regimes, and the

different pre-treatments in both species of *Solanum*. The seeds of *S. betaceum* and *S. quitoense* were dormant, and less dormancy was found in the cultivars Tamarillo of *S. betaceum* and common lulo (*S. quitoense*).

Dormancy was broken successfully for the *S. betaceum* and *S. quitoense* seeds. In both species, the best temperature to promote seed germination was the alternating temperature (25/15°C) for all treatments and seed lots. At constant temperatures, the promotion of germination was lower for the dry and water controls, meanwhile, gibberellic acid had a substantial, positive effect. However, the action of alternate temperature and gibberellic acid at the same time did not provide additional benefits to germination. Also, for both species, the gibberellic acid positively affected the rate of germination at all temperatures, particularly at 25/15 and 25°C.

One way to release seed dormancy in other *Solanum* species is alternating temperatures; e.g. *S. elaeagnifolium* (Trione and Cony, 1990), and *S. physalifolium* (Monte and Tarquis, 1997) with amplitudes exceeding 5°C. Alternating temperatures occur in the natural tropical Andean ecosystem where *S. betaceum* and *S. quitoense* crops are cultivated. Thus, choosing the minimum, mean and maximum temperatures of the Andean ecosystem for the germination test (Vargas-Figueroa and Torres-González, 2018) was a clue to obtaining successful germination for this species.

On the other hand, potassium nitrate (1%) promoted seed germination of the *S. betaceum* seeds at both constant and alternating temperatures. However, potassium nitrate promoted seed germination in *S. quitoense* only when the alternating temperature was applied, and, at the constant temperature, there was no promotion by potassium nitrate at all. These results agree with Yogeeshia *et al.* (2006), who broke seed dormancy in two cultivars of *Solanum melongena* L. with gibberellic acid; however, potassium nitrate only improved germination to some extent. In this sense, these results agree with the results of Wei *et al.* (2010), who promoted germination in *S. lycopersicum* with gibberellic acid in higher percent (>98%) than with potassium nitrate (>70%). Also, the application of gibberellic acid to the *S. lycopersicum* seeds produces seedlings with higher vigor (Balaguera-López *et al.*, 2009).

These results confirm the study of Cárdenas *et al.* (2004) on *S. betaceum* and *S. quitoense*, where dormancy was broken by an alternating temperature regime of 28/24 °C (12/12 h). They found a similar benefit for these species from GA<sub>3</sub> (1,000 mg L<sup>-1</sup>), but, in the present study, a slight increase in the germination was obtained for *S. betaceum* with GA<sub>3</sub> at a higher concentration (2,000 mg L<sup>-1</sup>). However, these results

contradict their results of declining germination with the application of KNO<sub>3</sub> (2%), perhaps because a lower concentration was used (1%). The positive response of the *Solanum* species studied here, and in other research, to gibberellins and nitrate in breaking seed dormancy shows the presence of a shallow seed dormancy, which is a result of gene expression (Finch-Savage and Footitt, 2017).

There was a difference in the promotion of germination between the cultivars of both species. *S. betaceum* cv. Tamarillo achieved higher germination than the common cultivar. However, the rate of germination was very similar for both cultivars. On the other hand, the common cultivar of *S. quitoense* had higher germination and rate of germination than cv. La Selva. The most commercial cultivars of these fruits seem to provide the highest germination results. This is because *S. quitoense* cv. La Selva is a cross between the cultivated species and a wild species (Fory, 2010) and an inter-specific hybrid that is much less cultivated. On another hand, *S. betaceum* cv. Tamarillo is a very high-yielding variety that produces large bright red fruits, and, of all varieties of this crop, it is one of the most rewarding and cultivated (The Climbing Fig, 2020).

## CONCLUSIONS

*S. betaceum* and *S. quitoense* exhibited shallow seed dormancy, and less dormancy was found in the more commercialized cultivars, such as *S. betaceum* cv. Tamarillo and *S. quitoense* (*i.e.* common cultivar). For both species, the most recently harvested seeds had more promotion of germination than the seeds stored for several months at the low seed moisture content (4%) and low storage temperature (20°C). Despite this, the storage conditions did not have a detriment on the seed germination of the tomato tree and lulo.

The seed dormancy of *S. betaceum* and *S. quitoense* was broken successfully by applying gibberellic acid (2,000 mg L<sup>-1</sup>) or alternating temperatures, particularly 25/15°C. The application of one or another treatment was enough because both treatments at the same time did not have an additional benefit for promoting seed germination. Meanwhile, the application of gibberellic acid increased the rate of germination more than potassium nitrate, at all temperatures. However, potassium nitrate (1%) promoted the seed germination of *S. betaceum* seeds at both constant and alternating temperatures and of

*S. quitoense* seeds only when the alternating temperature was applied.

The suggestion is for farmers to apply any of these treatments that work well at breaking seed dormancy in *S. betaceum* and *S. quitoense*; the most convenient option could be selected depending upon budget and other resources.

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**Conflict of interest.** The manuscript was prepared by the author, who declares that she has no conflicts of interest that put at risk the validity of the results presented here.

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