

LUMINOSITY, TEMPERATURE, AND SUBSTRATES ON THE
GERMINATION OF *Solanum capsicoides*

Julcinara Oliveira BAPTISTA¹ , Rodrigo Sobreira ALEXANDRE² , Paula Aparecida Muniz DE LIMA¹ ,
Simone de Oliveira LOPES³ , Caroline Palacio DE ARAUJO⁴ ,
Conceição de Maria Batista DE OLIVEIRA¹ , José Carlos LOPES⁵ 

¹ Postgraduate Program in Agronomy, Federal University of Espírito Santo, Alegre, Espírito Santo, Brazil.

² Department of Forestry and Wood Sciences, Federal University of Espírito Santo, Jerônimo Monteiro, Espírito Santo, Brazil.

³ São Carlos Metropolitan College, Bom Jesus do Itabapoana, Rio de Janeiro, Brazil.

⁴ Postgraduate Program in Forest Sciences, Federal University of Espírito Santo, Jerônimo Monteiro, Espírito Santo, Brazil.

⁵ Department of Graduate Studies in Agronomy, Federal University of Espírito Santo, Alegre, Espírito Santo, Brazil.

Corresponding author:

Julcinara Oliveira Baptista
julcinarabaptista@hotmail.com

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Abstract

Solanum capsicoides, commonly known as red soda apple, is a little-studied species with phytotherapeutic characteristics of interest to the pharmaceutical industry. However, little is known about its agronomic characteristics. Therefore, this study aimed to assess the effect of light, different temperatures, and substrates on the germination of *S. capsicoides* seeds. The study consisted of two experiments: Experiment I - Germination of *S. capsicoides* seeds under different wavelengths. The seeds were kept on Petri dishes covered with Gemitest™ paper moistened with distilled water and exposed to the monochromatic, red, far-red, and dark wavelengths. The experiment was performed in a completely randomized design with four replications of 25 seeds. Experiment II - Germination of *S. capsicoides* seeds on different substrates and at different temperatures. The seeds were distributed according to six substrates: paper roll, on paper, between sand, on sand, on soil + sand + manure, and between soil + sand + manure. The seeds were also subjected to the constant temperatures of 20, 25, 30, and 35 °C and the alternate temperatures of 20-30, 20-35, 25-30, and 25-35 °C, characterizing a 6 x 8 factorial arrangement. Germination rate, germination speed index, and mean germination time were evaluated. Red soda apple seeds are classified as positive photoblastic, with the highest germination rate occurring at the temperature of 20-35 °C combined with on paper, paper roll, on sand, and between sand substrates.

Keywords: Germination potential. Herbal medicines. Seeds.

1. Introduction

Solanum capsicoides All. is a species of the Solanaceae family, commonly known as red soda apple or gogoia. In Brazil, it is mostly distributed in the north-central region of the state of Santa Catarina (Batista-Franklin 2008). It is a shrub up to 1.20-m high with spiny leaves and branches and smooth orange-colored fruits containing elongated and ellipsoid seeds (Ferreira et al. 2013).

The use of native species with some medicinal properties has prevailed in the Brazilian population due to the many benefits to human health. They are used for therapeutic purposes, which considers medicinal plants, plant species cultivated or not; and for phytotherapeutic purposes, which considers

products obtained from medicinal plants or its parts, with prophylactic, curative, or palliative functions including medicine and traditional herbal products (Brasil 2014).

The extraction of leaf compounds characterizes the red soda apple as a phytotherapeutic plant with an antihypertensive effect, reducing cardiac hypertrophy and improving vascular function (Simões et al. 2016). It also contains antidepressant compounds such as cilistol A, astragalin, and cilistadiol, and the absence of toxicity, allowing the replacement of old compounds used in the production of antidepressant drugs with side effects that lead to treatment discontinuation (Petreanu et al. 2019).

Little is known about *S. capsicoide*, thus understanding the germination and vigor of *S. capsicoide* seeds is important to develop improved seed germination protocols for this species for both medicinal and commercial uses. Germination is extremely important in the plant life cycle, and well-succeeded germination is required for a satisfactory plant establishment. Several factors affect germination, such as substrate, water, temperature, light, and oxygen. Under appropriate soil and environment conditions, germination occurs through water absorption by the seed, determining the beginning of embryonic axis elongation and culminating in radicle protrusion (Bewley et al. 2013), as observed in seeds of *Apuleia leiocarpa* (Spadeto et al. 2018) and *Enterolobium maximum* (Farias et al. 2019).

During this phase, water deficit affects germination rate, speed, and uniformity. This is observed for *Lavandula mairei* Humbert, a species considered medicinal, rare, and endangered, endemic to Morocco, from which recent germination studies were performed on the conservation of species that showed that a decrease in water potential from -0.53 MPa reduced the germination rate by around 11% (Hamdaoui et al. 2021). Another factor is the type of substrate, which must be selected by considering the size and aeration of seeds, the demand for water supply, water retention capacity, the presence or absence of light sensitivity, and the easiness to count and evaluate seedlings (Brasil 2009). The seed responses differ for the type of substrate, as observed in *Jacaranda micrantha* seeds, whose recommended substrates are on sand and Germitest™ paper sheets (Bovolini et al. 2015), while *Callisthene major* var. *pilosa* seeds require a between paper substrate for the germination test (Oliveira et al. 2020).

The seeds of several species show different temperature ranges for germination, namely minimum, maximum, and optimum temperatures. The minimum temperature is that below which germination does not occur because the speed of germination processes is zero, the maximum temperature is that above which germination does not occur, and the optimum temperature is that in which the germination process occurs with higher intensity and speed. Furthermore, the temperature may change or delay the biochemical processes of the seeds, delaying seed metabolism and inhibiting germination (Bewley et al. 2013; Yang et al. 2020).

Luminosity is essential for seed germination in some species, and the effect of light on germination varies according to irradiance, intensity, and time of exposure. Furthermore, the promotion of germination by light is mediated by phytochromes, which are pigments that work on the plasma membrane, regulating substance permeability and flow (Bae and Shoi 2008). The phytochrome is a photoreceptor system whose action depends on the type of incident radiation. The red phytochrome absorbs light more intensely in the red regions, with an absorbance peak at 660 nm, converting it into the active form; and the far red, with an absorbance peak at 730 nm, converts the active form into inactive. When phytochromes detect the red-to-red ratio far from incident light, they promote germination through the low fluence response (Shinomura et al. 1994).

Species that expand light for germination are classified as positive photoblastic, while others are negative photoblastic and germinate under light limitations; there are also indifferent seeds, with no light sensitivity (Baskin and Baskin 2001). Additionally, there is a potential relationship between seed size and the need for light to promote germination, in which small seeds usually have a lower nutrient reserve and need to be sown in upper layers that receive light and because they lack the support for disrupting the lower layers of soil (Gul et al. 2013). Thus, considering light sensitivity, the need for studies on seed germination becomes evident, especially due to the varied seed responses (Brasil 2009; Bewley et al. 2013; Taiz et al. 2017).

Therefore, this study aimed to evaluate the effect of light, different temperatures, and substrates on the germination of *S. capsicoide* seeds.

2. Material and Methods

The experiment was performed in the Laboratory of Seed Technology and Analysis, Department of Agronomy, at the Federal University of Espírito Santo (UFES), Alegre, ES, Brazil. The *S. capsicoides* seeds were obtained from plants located at the Córrego do Feijão Cru stream (20° 32' 29" S and 41° 40' 06" W) in an Atlantic Forest reservation located at Pico da Bandeira, Mountain Region of Caparaó, city of Ibitirama, ES, Brazil. Mature plants and red-colored fruits were collected, and seeds were extracted manually.

Biometry and physical characterization of fruits and seeds

The biometric analyses were performed using four replicates of 10 fruits and 25 seeds. The length, width, thickness, and mass were determined with the help of a 6" digital caliper (Zaasprecision) with a precision of 0.01 mm and analytical balance (0.0001 g). The seed water content was determined with the air-oven method using two sub-samples of 25 seeds (105 ± 3 °C/24 hours) (Brasil 2009). The 1000-seed mass was determined using eight sub-samples of 100 seeds in a precision analytical balance (0.0001 g). The mean weight was expressed as grams seeds⁻¹. The number of seeds was calculated based on the mass of 1000 seeds and expressed in kg⁻¹ (Brasil 2009).

Experiment I: Germination of seeds under different wavelengths

The seeds were disinfected by immersion in 70% alcohol (v/v) for one minute, followed by a 2% sodium hypochlorite solution (v/v) for three minutes, and washed three times with distilled water for residue removal. The seeds were placed on Petri dishes for the germination tests on two sheets of Germitest™ paper previously moistened with a volume of distilled water equivalent to 2.5 times the dry paper mass. Subsequently, the Petri dishes were maintained under different luminosity conditions: dark, red, far-red, and monochromatic light, and under a constant temperature of 20 °C, in B.O.D. (Biochemical Oxygen Demand) germination chambers.

In monochromatic light, the Petri dishes were exposed to direct light under four Sylvania™ 20 W fluorescent lamps. In red wavelength, the Petri dishes were covered with two red cellophane sheets and maintained under Sylvania™ 20 W fluorescent lamps. In far-red wavelength, the Petri dishes were covered with blue and red cellophane sheets and exposed under white incandescent lamps. In the dark wavelength, the Petri dishes were covered with two black polyethylene bags and the readings were performed under a green safety light.

Germination was monitored daily up to 21 days after sowing. The seeds were considered germinated when the primary root had ≥ 2 mm. The variables studied were germination rate (%), germination speed index (GSI) (Maguire 1962), and mean germination time (Labouiau 1983). The experimental design was completely randomized, with four replications of 25 seeds.

Experiment II: Germination of seeds on different substrates and at different temperature regimens

In this study, the seeds were sown in the following substrates: paper roll (PR), prepared with overlapped Germitest™ paper sheets, covered by a third sheet, moistened with a volume of distilled water equivalent to 2.5 times the dry paper mass, and maintained in transparent plastic bags to prevent water loss by evaporation; on paper (OP), sown in Petri dishes covered with two Germitest™ paper sheets moistened with a volume of distilled water equivalent to 2.5 times the dry paper mass; between sand (BS) and on sand (OS); and between and on soil + sand + manure - B (S + S + M) and O (S + S + M) -, respectively, at a ratio of 1:1:1. The sand and soil + sand + manure substrates were maintained in Gerbox™ boxes, moistened at 60% of the moisture-holding capacity, and sowing was performed at 1 cm of depth. The temperatures tested were constant temperatures of 20, 25, 30, and 35 °C, and alternate temperatures of 20-30, 20-35, 25-30, and 25-35 °C, with a 12-hour photoperiod.

Similarly, germination was monitored daily up to 21 days after sowing by analyzing germination rate (%), germination speed index (GSI) (Maguire 1962), and mean germination time (MGT) (Labouriau 1983).

The experimental design used was completely randomized, in a 6 x 8 factorial arrangement (six substrates x eight temperatures), and with four replications of 25 seeds.

The results obtained were subjected to the analysis of variance and the means were compared by Tukey's test at a 5% probability. The data referring to the characteristics analyzed were transformed: germination $Y = [\arcsine (x/100) 1/2]$, and the remainder by $[(x + 0.5) 1/2]$, observing the assumptions of the tests of normality, variance homogeneity, and regression analysis for the quantitative data. The R software was used for the statistical analyses (R Core Team 2020).

3. Results

Experiment I: Germination of seeds under different wavelengths

The *S. capsicoide* seeds are brownish, spherical to reniform, with length and width of approximately 27.974 ± 0.82 and 24.018 ± 0.99 mm, respectively, fruit mass of 8.748 ± 1.03 g, and mean of 337 ± 19 seeds per fruit, totaling 408,163 seeds per kg and 1000-seed mass of 2.45 g (Table 1).

Table 1. Physical characteristics of *Solanum capsicoide* All. fruits and seeds.

Parameters	Values
Fruit length (mm)	27.974 ± 0.82
Fruit width (mm)	24.018 ± 0.99
Fruit mass (g)	8.748 ± 1.03
Seed moisture (%)	13 ± 1.03
Length/Width (mm)	1.16 ± 0.03
Thickness (mm)	3.28 ± 0.37
Mean number of seeds per fruit	337 ± 19
Number of seeds kg^{-1}	408.163
1000-seed mass (g)	2.45

The highest mean germination rates were found when subjecting *S. capsicoide* seeds to red and white wavelengths (100 and 99%, respectively) (Table 2).

Table 2. Germination (%) and germination speed index (GSI) of *Solanum capsicoide* All. seeds under different wavelengths.

Wavelength	Germination (%)	GSI
Dark	0.0 b ⁽¹⁾	0.000 ^b
Red	100.0 ^a	3.153 ^a
Far-red	0.0 ^b	0.000 ^b
Monochromatic light	99.0 ^a	3.003 ^a

⁽¹⁾Means followed by the same letter do not differ at a 5% probability by Tukey's test.

Experiment II: Germination of seeds on different substrates and at different temperature regimens

High germination rates were found when subjecting *S. capsicoide* seeds to an alternating temperature of 20-35 °C, with means above 97% when combined with the paper roll, on paper, between sand, and on sand substrates (Table 3). However, for the on paper substrate, the temperature of 20-35 °C did not differ statistically from the temperatures of 20, 25, and 35 °C (Table 3).

There was no difference for the temperatures of 20, 35, 20-30, and 20-35 °C combined with the between paper, paper roll, and between sand substrates, which resulted in a higher germination mean and germination speed index (Tables 3 and 4). These same substrates showed an acceleration in germination days (Figures 1 A, B, and C).

For the between soil + sand + manure and on soil + sand + manure substrates, the temperatures of 20 and 20-35 °C resulted in a higher germination mean and speed index. However, when *S. capsicoide* seeds were subjected to other temperatures, they obtained lower germination means (Table 3) and consequently the lowest germination speed indices (Table 4). This substrate also showed slow and uneven germination (Figures 1E and F), with a mean germination time of approximately 19 days (Table 5).

Table 3. Germination (%) of *Solanum capsicoides* All. seeds on different substrates and at different temperature regimens.

T (°C)	Germination (%)					
	Substrates					
	PR	OP	BS	OS	B (S + S + M)	O (S + S + M)
20	100 ^{Aa(1)}	100 ^{Aa}	43 ^{Cb}	99 ^{Aab}	19 ^{Cab}	79 ^{Ba}
25	66 ^{Bb}	92 ^{Aabc}	11 ^{Dc}	67 ^{Bde}	14 ^{CDabc}	39 ^{BCbc}
30	0 ^{Bc}	30 ^{Ae}	20 ^{Bc}	38 ^{Ae}	1 ^{Bcd}	0 ^{Be}
35	88 ^{Aabc}	93 ^{Aab}	56 ^{Bb}	86 ^{Abcd}	0 ^{Dde}	25 ^{cd}
20-30	87 ^{Aab}	68 ^{ABcd}	45 ^{Bb}	87 ^{Abcd}	5 ^{Cbcd}	4 ^{Ce}
20-35	98 ^{Aa}	97 ^{Aa}	100 ^{Aa}	100 ^{Aa}	29 ^{Ca}	62 ^{Bab}
25-30	86 ^{Aab}	50 ^{Cde}	60 ^{Bcb}	81 ^{ABcd}	4 ^{Dbcd}	12 ^{Dde}
25-35	95 ^{Aa}	76 ^{Bbcd}	75 ^{Bb}	94 ^{ABabc}	11 ^{Dabcd}	41 ^{Cbc}

⁽¹⁾Means followed by the same uppercase letter in the row and lowercase letter in the column do not differ at a 5% probability by Tukey's test. Legend: T. Temperature (°C), PR (paper roll), OP (on paper), BS (between sand), OS (on sand), B (S + S + M) (between soil + sand + manure), O (S + S + M) (on soil + sand + manure).

Table 4. Germination speed index (GSI) of *Solanum capsicoides* All. seeds on different substrates and at different temperature regimens.

T (°C)	Germination speed index (GSI)					
	Substrates					
	PR	OP	BS	OS	B (S + S + M)	O (S + S + M)
20	1.434 ^{ABCa(1)}	1.467 ^{ABa}	1.133 ^{CDabc}	1.620 ^{Aa}	0.823 ^{Dab}	1.218 ^{BCa}
25	1.178 ^{ABa}	1.417 ^{Aab}	0.872 ^{Bcc}	1.115 ^{ABb}	0.315 ^{Dcd}	0.594 ^{CDcd}
30	0.000 ^{Bb}	0.871 ^{Ac}	0.026 ^{Bde}	0.741 ^{Ac}	0.013 ^{Bde}	0.000 ^{Be}
35	1.390 ^{ABa}	1.456 ^{Aa}	1.080 ^{Bbc}	1.519 ^{Aa}	0.000 ^{Dde}	0.557 ^{Ccde}
20-30	1.301 ^{ABa}	1.206 ^{ABabc}	1.070 ^{Bbc}	1.536 ^{Aa}	0.482 ^{Cbc}	0.259 ^{Cde}
20-35	1.464 ^{Ba}	1.431 ^{BCab}	1.459 ^{Ba}	1.827 ^{Aa}	1.069 ^{Da}	1.125 ^{CDab}
25-30	1.340 ^{ABa}	1.106 ^{Bbc}	1.109 ^{Bbc}	1.499 ^{Aa}	0.236 ^{Ccde}	0.501 ^{Cd}
25-35	1.353 ^{Ba}	1.156 ^{BCabc}	1.306 ^{Bab}	1.708 ^{Aa}	0.487 ^{Dbc}	0.872 ^{Cbc}

⁽¹⁾Means followed by the same uppercase letter in the row and lowercase letter in the column do not differ at a 5% probability by Tukey's test. Legend: T. Temperature (°C), PR (paper roll), OP (on paper), BS (between sand), OS (on sand), B (S + S + M) (between soil + sand + manure), O (S + S + M) (on soil + sand + manure).

Table 5. Mean germination time (MGT) of *Solanum capsicoides* All. seeds on different substrates and at different temperature regimens.

T (°C)	Mean germination time (MGT)					
	Substrates					
	PR	OP	BS	OS	B (S + S + M)	O (S + S + M)
20	17 ^{Cc(1)}	17 ^{Cc}	15 ^{Dd}	19 ^{Bb}	19 ^{Bb}	20 ^{Ab}
25	17 ^{Dc}	17 ^{Cd}	18 ^{Ca}	19 ^{Bb}	19 ^{Bb}	20 ^{Ab}
30	0 ^{Dd}	18 ^{Bb}	17 ^{Cb}	19 ^{Ab}	0 ^{Dc}	19 ^{Ac}
35	18 ^{Cb}	17 ^{Dc}	15 ^{Ed}	20 ^{Aa}	19 ^{Bb}	0 ^{Fd}
20-30	19 ^{Ca}	19 ^{Ca}	16 ^{Dc}	19 ^{Cb}	20 ^{Ba}	21 ^{Aa}
20-35	17 ^{Cc}	17 ^{Cc}	14 ^{De}	17 ^{Cd}	19 ^{Bb}	20 ^{Ab}
25-30	18 ^{Cb}	19 ^{Ba}	15 ^{Dd}	18 ^{Cc}	20 ^{Aa}	20 ^{Ab}
25-35	18 ^{Bb}	18 ^{Bb}	15 ^{Cd}	18 ^{Bc}	19 ^{Ab}	19 ^{Ac}

⁽¹⁾Means followed by the same uppercase letter in the row and lowercase letter in the column do not differ at a 5% probability by Tukey's test. Legend: T. Temperature (°C), PR (paper roll), OP (on paper), BS (between sand), OS (on sand), B (S + S + M) (between soil + sand + manure), O (S + S + M) (on soil + sand + manure).

Regardless of the type of substrate used, the temperature of 30°C affected negatively the germination of *S. capsicoides* seeds, resulting in low germination rates and consequently lower germination speed index values, except for substrate B (S + S + M), which showed the lowest means at the temperature of 35°C (Tables 3 and 4).

The lowest mean germination time was found with the between sand substrate, resulting in germination around 15 days (Table 5). This substrate provided 100% germination at a temperature of 20-35°C (Table 3), with a mean germination time of 14 days (Table 5). At the same temperature, the on sand

substrate also resulted in 100% germination (Table 3) but there was a 3-day difference in mean germination time (Table 5).

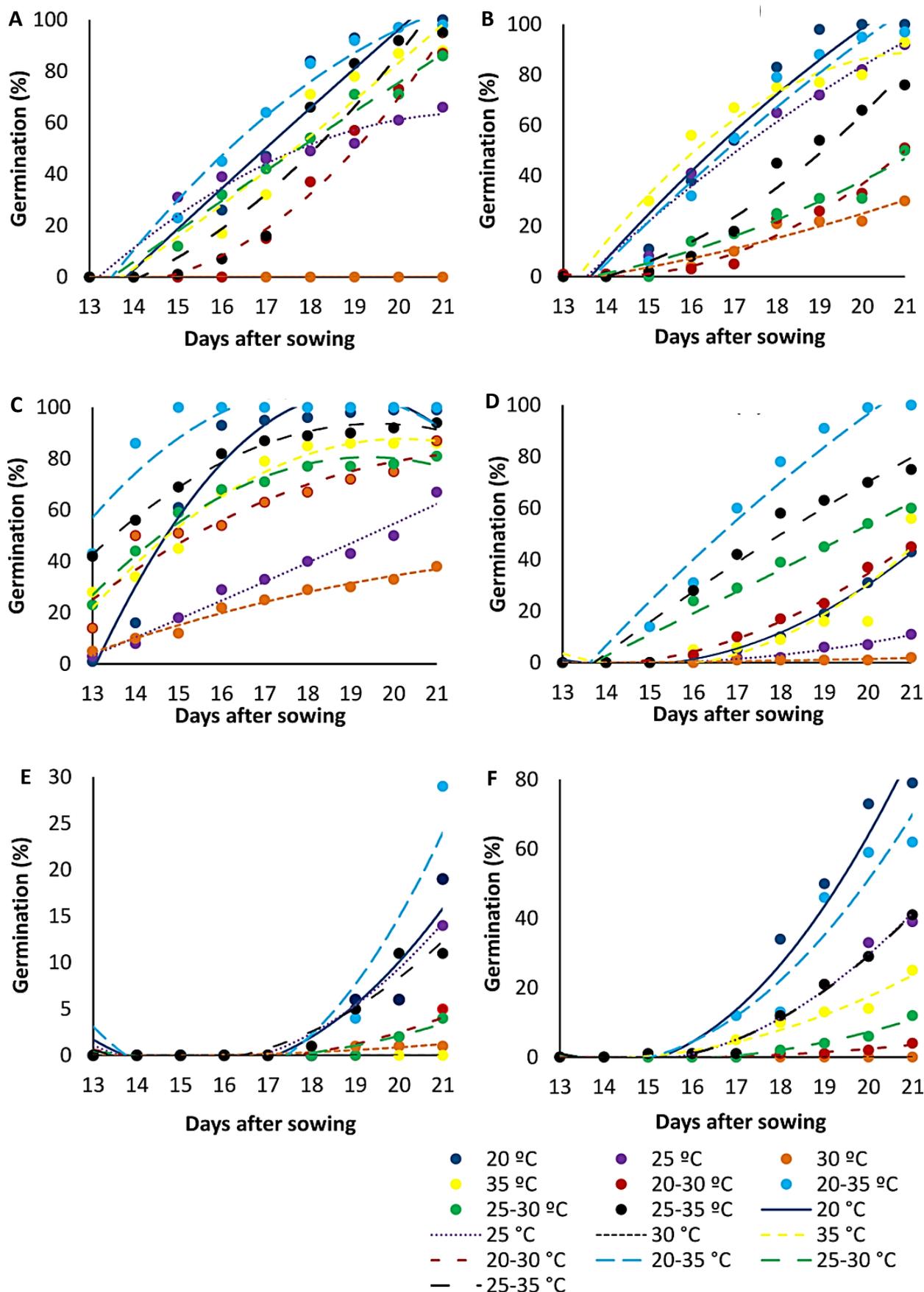


Figure 1. Germination (%) of *Solanum capsicoide* All. seeds on different substrates and at different temperature regimens. Substrates: A - paper roll; B - on paper; C - between sand; D - on sand; E - between soil + sand + manure; F - on soil + sand + manure.

The on sand substrate reached maximum seed germination (100%) around 15 days and 20-35°C (Tables 3 and 5). However, the on sand substrate did not show a statistical difference between the temperatures. At all the temperatures studied in this substrate, germination started early compared to the remaining substrates (Figures 1C and 1D).

In the soil + sand + manure substrate, the germination rates were statistically lower, highlighting the between soil + sand + manure substrate, in which, regardless of the temperature used, germination rates were lower than 30% (Table 3) and the mean germination speed indices were low (Table 4). These results can also be seen in Figures 1E and 1F, with a significant delay in the germination process, especially in the soil + sand + manure substrate (Figure 1E).

It is also noteworthy that when subjecting red soda apple seeds to a combination of 35°C temperature and between soil + sand + manure substrate and a combination of 30°C temperature and on soil + sand + manure substrate, seed germination was completely inhibited (Table 3).

4. Discussion

Experiment I: Germination of seeds under different wavelengths

The *S. capsicoides* fruits are small, spherical, and composed of a high number of seeds per fruit (Table 1). Chiarini and Barboza (2009) described the characterization of fruits of this genus as berries containing seeds embedded in a solid fleshy mass and with an epicarp less than 2-mm thick. The fruit color ranges from orange to red, with winged seeds, exocarp containing an undulate cuticle, epidermis with 1-2 layers of orange-colored brachysclereids, hypodermis with a sclerified sclerenchyma, and the mesocarp composed of 20 layers of spongy tissue over the veins and 20 underneath them.

The germination tests allowed verifying cryptocotyledonary and hypogeal germination in *S. capsicoides* seeds with an imbricate embryo. These are characterized by epicotyl elongation, maintaining the seed below the substrate surface during the germination process (Duke 1969).

The red soda apple seeds depend on light to germinate and are considered positive photoblastic for responding positively to light stimulation. Consequently, germination does not occur when subjected to far-red and dark wavelengths (Table 2). The light quality and length of the LED are related to morphological and biochemical parameters such as in the alteration of germination and seed growth and development, which characteristics can be improved when using the ideal light length (Simlat et al. 2016).

In *Stevia rebaudiana* Bertoni seeds at 20°C, using Germitest™ paper as a substrate, the favorable effect on germination was caused by the blue LED light and the combination of red and white LED lights, also observing that, when exposed to blue LED light, germination rate and germination speed index values were higher. Furthermore, it provided seedlings with higher quality, a higher number of seeds and roots, and stomatal frequency, besides providing high pigment concentrations and high activity of antioxidant enzymes catalase and peroxidase, which is important for tissue protection against reactive oxygen species (Simlat et al. 2016).

Poor seed germination of some species may occur due to biotic factors such as the genotype, and abiotic factors such as temperature, water, and light (Li and Yang 2020). The latter is one of the most important environmental factors for the growth and development of seedlings (Daud et al. 2013). Additionally, plants can respond to light intensity and quality because, in response to the stress caused by light, plants produce different reactive forms of oxygen, which are the main causes of damage to plants, modifying metabolic processes such as the reduction of the photosynthetic rate of plants (Dong et al. 2014). The *Lactuca sativa* seeds showed that light induced the production of nitric oxide, a gaseous signaling molecule that regulates plant growth and development and stress responses in plants, which, in turn, is associated with the formation of phosphatidic acid, an important amplifier of abscisic acid signaling in plants (An and Zhou 2016).

Experiment II: Germination of seeds on different substrates and at different temperature regimens

The red soda apple seeds submitted to alternating temperatures relative to constant temperatures and the use of on paper, paper roll, between sand, and on sand substrates provided higher mean germination rates (Table 3), germination speed index (Table 4), and mean germination time (Table 5). These superior results for the type of substrate can be justified by the better structure, aeration, and water retention capacity, thus maintaining proper conditions for seedling germination and development. Moreover, these substrates provide an adequate contact area between the substrate and the seed, allowing greater water absorption and consequently higher germination rates (Reis et al. 2020).

The paper roll substrate provided a higher rate of germination speed (Table 3), possibly because red soda apple seeds are small and the paper roll substrate provides a greater contact between the substrate and the seed (0,5 cm), allowing greater water retention. Oliveira et al. (2016) studied the combination of the temperatures of 25, 30, 35, and 25-35°C with paper roll, on paper, sand, on sand, and on vermiculite substrates in the germination of *Simira gardneriana* M. R. Barbosa & Peixoto seeds. The authors verified that, in the paper roll substrate, *S. gardneriana* seeds achieved high germination rates at the temperatures of 25, 30, and 25-35°C, but germination was low at 35°C, achieving the respective values of 84, 82, 71, and 39%. This showed that ideal temperatures combined with substrates with good physical, chemical, and structural characteristics provide high germination rates.

This result can be explained by the on sand substrate providing greater porosity and aeration, and the paper roll substrate with greater water retention, thus allowing the seed to obtain the maximum germination rate, which starts with water absorption and ends with radicle protrusion (Bewley et al. 2013). This germination process is characterized by three phases. First is the imbibition phase, which shows a rapid water uptake and seed swelling, followed by a plateau. In this phase of metabolic activation and a later marked absorption of water, protrusion occurs from the radicle and this water absorption process starts near the micropyle (Steinbrecher and Leubner-Metzger 2017).

Temperature is one of the most important abiotic factors in seed germination, as it affects speed, time, uniformity, and rate of germination, and the relationship with local temperature conditions determines the adaptability of species to climate change (Seguí et al. 2021).

The alternation of temperatures for some species is crucial for obtaining high germination rates, corresponding to the fluctuations observed in the environment, and it can work on seed coating, making it more permeable to water and oxygen (Bewley et al. 2013; Taiz et al. 2017). Temperature also works directly in response to physiological and biochemical processes inside the seeds, as high temperatures can increase the respiratory rate of seeds and trigger an increase in reactive oxygen species, which may damage organelles, nucleic acids, lipids, and proteins, and consequently cause rapid seed deterioration and loss of viability (Silva et al. 2020).

The alternation of temperatures in the present study provided high germination rates of *S. capsicoide* seeds, especially at a temperature of 20-35°C. Ozden et al. (2021) investigated the effect of alternating temperatures on germination, emergence, and physiological changes that regulate dormancy in *Solanum melongena* seeds and found high rates of germination (92%) and emergence (88%) of seeds at the alternating temperature of 35-20°C. They also showed positive correlations with enzymatic and hormonal fluctuations in seeds, such as decreased lipase enzyme activity and abscisic and jasmonic acid contents that work as signaling molecules and regulate seed dormancy.

The relationship between temperature and different substrates is mainly related to soil moisture, as it may affect physiological and biochemical processes in seeds (Carvalho and Nakagawa 2012). Thus, it is necessary to use substrates with a low degree of pathogenic agents and good aeration and drainage that allow the passage of light, providing high germination rates (Afonso et al. 2012).

The substrate composed of soil + sand + manure in the conditions of composition and temperature studied were not satisfactory for the germination of *S. capsicoide* seeds. This may be explained by the microbial activity of the substrate caused by cattle manure, possibly delaying germination by reducing seed viability and consequently germination rate and speed. Furthermore, the presence of these harmful phytopathogenic microorganisms causes seed deterioration, which leads to their death. These seeds were visibly deteriorated, with symptoms of fungal attack.

This substrate has greater water retention due to its manure composition, which is the main source of organic matter, potentially favoring germination in some species. Moreover, organic matter improves the physical, chemical, and biological properties of the soil (Bernardino et al. 2018). However, due to its rich organic matter composition, it may cause seed deterioration for some species, as verified in this study.

5. Conclusions

The *S. capsicoides* seeds are classified as positive photoblastic.

The *Solanum capsicoides* seeds submitted to a temperature of 20-35°C have higher germination rates.

The paper roll, on paper, between sand, and on sand substrates combined with the temperature of 20-35°C were favorable to seed germination and the early development of *S. capsicoides* plants.

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