



## Article

# Maternal Environment and Priming Agents Effect Germination and Seedling Quality in Pitaya under Salt Stress

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**Abstract:** Lack of water and salinity are common problems in many parts of the world. Therefore, some types of cacti can present as promising crops. Therefore, the ability of cactus species to survive and adapt under natural stress conditions should be evaluated. The experiment was aimed at evaluating the effect of salt stress on germination and emergence of pitaya seeds obtained from different species (*Hyloceresu undatus* (Haw.) Britton and Rose and *Hylocereus polyrhizus* (Lem.) Britton and Rose), priming with plant growth regulators, namely salicylic acid (SA), oxalic acid (OA) and mepiquat chloride (MC). The experiment had a completely randomized design with a 2 × 4 × 3 factorial scheme corresponding to two pitaya cultivars (white- and red-fleshed), four NaCl concentrations (0, 2500, 5000 and 10,000 ppm), and three PGRs (150 ppm/MC, SA, OC). According to the results, the maternal environment of the seed was important in salt stress resistance, while seeds matured in the environment with red fruit flesh were more tolerant to salt stress. Although Pitaya species are relatively salt-tolerant, growth (about 30%) was significantly reduced above 2500 ppm and germination (about 45%) above 5000 ppm. Germination percentage stood out as the most important trait determining seed quality and had positive effects on the germination stress tolerance index (r: 0.63), seedling length (r: 0.74) and fresh seedling weight (r: 0.56). This is the first study of how maternal environment affects germination and seedling quality under saline conditions in *Hylocereus*. The results obtained may contribute to pitaya cultivation and breeding.

**Keywords:** Cactaceae; seed viability; seedling quality; salinity; PGRs; *Hylocereus* sp.



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## 1. Introduction

Pitaya, known as dragon fruit, is in the genus *Hylocereus*, which is represented by four species according to their peel and flesh color, namely: *H. undatus* (Haw.) Britton and Rose, *H. polyrhizus* (Syn. *H. monacanthus*), *H. costaricensis* (FAC Weber) Britton and Rose and *H. megalanthus* (K. Schum. ex Vaupel) Ralf Bauer (Syn. *Selenicereus megalanthus*) [1]. *Hylocereus* is a former genus of epiphytic cacti, commonly known as night-blooming cactus (though the word is also applied to many other cacti). Several species previously assigned to the genus produce big edible fruits known as pitayas, pitahayas, or dragon fruits. Fruits of these species are popularly consumed due to their aroma. In addition, in the current pandemic, the consumer's interest in pitaya fruit, which is rich in chemicals with high antioxidant effects such as phenols, organic acids, minerals and vitamins, has increased [1–3]. This antioxidative effect has been proven to prevent many diseases [4,5]. The fruit peel of pitaya, which contains more than 50% unsaturated fatty acids (linoleic and linolenic) in their seeds [6], is a source of pectin and is very important in food and textile dyeing with the natural colorants it contains [7]. The demands of pitaya, which has the potential for many different uses for nutraceutical and industrial purposes, has

increased, which is reflected in its production. As a matter of fact, all countries where pitaya is cultivated emphasize that the amount of production has increased compared to the previous years [8].

Sustainable and economic continuation of this high demand is only possible if breeders develop genotypes that meet the demands of producers, consumers and industry. For this reason, recently, efforts have been accelerated to develop early, middle and late varieties with high yield and attractiveness, resistant to biotic and abiotic stress conditions in combination, self-fertile, rich in chemicals with high antioxidant effects, suitable for different cultivation systems (open/greenhouse) [9]. Due to the quantitative nature of the desired traits and the complexity of inheritance mechanisms, hybrid breeding is still the most widely used method [10]. However, information on the factors affecting the germination of cactus seeds from the genus *Hylocereus* is very limited [11].

Germination depends on the chemical composition and testa permeability of the seed and favorable environmental conditions [12]. Salinity is a major environmental problem worldwide, especially in arid and semi-arid regions, limiting or making cultivation economically unfeasible. With global climate change, saline areas are expected to increase due to irrigation irregularity and high evaporation [13]. It has been pointed out that cactus species such as pitaya, which are particularly adaptable to different soil conditions, may be an alternative cultivation option for utilizing these areas [14,15]. However, research on how pitaya species/cultivars/genotypes perform under these stress factors is scarce. Pitaya seeds germinated under saline conditions reduced germination rate and seedling length up to 33% and 38%, respectively, according to cultivars [16]. It was emphasized that not only the shoot but also the root development regressed in all investigated hybrid pitaya genotypes under salt concentrations [17]. Also, the germination speed index decreased as the salt stress increased regardless of salt source, such as NaCl, MgCl<sub>2</sub> and KCl [17,18]. But no reports were found in the literature on the effects of the maternal environment on germination and seedling quality.

By acting on the osmotic potential of the substrate, salts reduce the potential gradient between the substrate and the seed surface, limiting water uptake by the seed and adversely affecting the plants developing from these seeds. They disrupt the ion balance and negatively affect stomatal movement and photosynthesis [19]. Enzyme activity is impaired, and metabolic activity is restricted. Increased reactive oxygen species disrupt cell integrity and homeostasis [20–22]. For these reasons, it is not possible to maintain production sustainably. Although salt stress occurs in all plants, tolerance levels and reduction in growth and development rates differ among species and phenological stages [23]. Studies on the germination response of seeds exposed to artificial stress conditions are important ecophysiological tools that can be used to understand the ability of species to survive and adapt to natural stress conditions. These tools are also used to assess the sensitivity of these species and their ability to survive and adapt to suppression when exposed to unfavorable and novel environments [24]. Therefore, although salinity has been extensively analyzed in cultivated species, the effects of NaCl in cacti are poorly documented.

The positive effects of exogenously applied growth regulators on sustainability have been demonstrated in studies with different species to increase plant tolerance to various abiotic stress factors [25]. Salicylic acid (SA), oxalic acid (OA) or mepiquat chloride (MC) applied to plants or seeds regulate stomatal movements and contribute to ion uptake and transport as important signaling molecules [26–28]. Through morphological, physiological, and biochemical pathways, salicylic acid (SA), a plant hormone, plays a key role in inducing plant defense against a variety of biotic and abiotic stressors. Moreover, SA stimulated cell division in seedlings and roots, resulting in greater plant growth [29]. Mepiquat chloride is a synthetic inhibitor of endogenous hormone, whereas chlormequat chloride is a chemical inhibitor of gibberellin. It is irreversible, unlike gibberellin, which can be applied to plants for increased fertility after over use of MC, which is a key distinction between the two plant growth hormones [30]. OA is a natural organic acid with numerous physiological roles, the most important of which is the promotion of systemic resistance to fungal and viral

infections via an increase in antioxidant enzymatic activities and phenolic compounds [31]. It was recently designated as a generally recognized safe (GRAS) substance. This molecule's antioxidant potential has been proven, and its role as a natural antioxidant compound in plant systems has been suggested [32]. It reduces the negative effects of reactive oxygen species (ROS) by protecting the structure and function of the cell membrane and increasing the synthesis of antioxidant-derived compounds. This allows the maintenance of osmolytes and homeostasis [33]. Plant growth regulators promote germination and development by maintaining photosynthetic activity [34–36], regulate the expression of genes involved in synthesizing vital amino acids under stress [37], restrict the development of different pathogens and have inducing effects on the acquisition of resistance [38–41].

This study evaluated the mitigating effect of some plant growth regulators on the performance of different pitaya species under different salt stress conditions during seed germination and seedling emergence periods under controlled laboratory conditions. Also, this is the first study conducted on how the maternal environment affects germination and seedling quality under saline conditions in *Hylocereus*.

## 2. Materials and Methods

### 2.1. Plant Materials

In the study, two different species, namely *H. undatus* (*Hu*) and *H. polyrhizus* (*Hp*) of the *Hylocereus* genus, were used as material. The plants were grown in Muğla province, which is located in the southwest of Turkey and has a subtropical climate. Ripe fruits of Siam Red (*Hp*, red peel color and red-fleshed) and Vietnam White (*Hu*, red peel color and white-fleshed) pitaya varieties. Seeds were obtained from fresh fruits of similar size that fully ripened on the plants. The fruits were peeled, and the seeds were separated from the pulp manually and washed with tap water several times to remove mucilage and the left-over pulp [16]. Seeds were treated with 2% sodium hypochlorite for 3 min for surface sterilization.

### 2.2. Preparing Solutions and Performing Seed Priming

The dried seeds were separated according to the treatment groups, weighed and placed in Petri dishes. Salicylic acid, mepiquat chloride or an oxalic acid solution with a concentration of 150 ppm (application concentration was determined by preliminary studies) was added to the Petri dishes at five times the seed weight [42]. The Petri dishes were wrapped with aluminum foil and kept in a growth chamber at 25 °C for 24 h.

### 2.3. Experimental Layout

Following the priming application, the seeds were counted and grouped. The study, carried out as a laboratory study, was designed with three replicates, and each replicate consisted of 50 seeds. The seeds of each replicate were homogeneously distributed in 3 layers of Whatman filter paper, 2 on the bottom and 1 on top of the seeds, and 7 mL of salt solution (2500 ppm, 5000 ppm, 10,000 ppm) or pure water (control) was applied to each filter paper (21 mL for each replicate at the start). The homogeneously soaked filter papers were folded into zip-lock bags to minimize moisture loss and placed in a growth chamber set at 25 °C, ~650 lux and 12/12 h photoperiod for germination [16,43]. Moisture was controlled, and the salt solutions were added to the filter papers according to their groups when necessary.

### 2.4. Germination-Related Traits

For 20 days, counts were made every day, and germination percentage (%), mean germination time and germination stress tolerance index were calculated at the end of the 20th day. On the 45th day following the establishment of the experiment, ten seedlings randomly selected from each replicate were measured for seedling shoot length (mm) using a caliper (Traceable—6, VWR International, Milan, Italy) sensitive to 0.01 mm and seedling fresh weight (mg) using a precision balance (Sartorius—CPA 16001S, Göttingen, Germany)

sensitive to 0.001 g. Then, the samples were kept in an oven at 70 °C for 48 h, and their dry weights were determined with the help of the same precision balance. As a result of the ratio of dry weight to fresh weight multiplied by 100, the amount of dry matter per unit amount was found as a percentage (%) [16].

Seeds with radicles reaching 2 mm in length were considered for all parameters. The germination percentage was determined according to ISTA [44] rules.

Mean germination time (MGT) was calculated to evaluate the speed of germination as defined by ISTA [44] with the following Formula (1), where n is the seed number germinated on day D, and D is the number of days from the beginning of the germination test.

$$\text{MGT} = \frac{\sum(Dn)}{\sum n} \quad (1)$$

The germination stress tolerance index (GSTI) was calculated as a percentage (%) by using Formula (2), where n is the number of seeds germinated at day d [45].

$$\text{GSTI} = \left[ \frac{\text{nd2} (1.00) + \text{nd4} (0.75) + \text{nd6} (0.5) + \text{nd8} (0.25) \text{ of stressed seeds}}{\text{nd2} (1.00) + \text{nd4} (0.75) + \text{nd6} (0.5) + \text{nd8} (0.25) \text{ of control seeds}} \right] \times 100 \quad (2)$$

### 2.5. Statistical Analysis

The experimental design was a 3-factor factorial, arranged in a completely randomized design with 3 replicates. Analysis of variance and comparison of means were performed by the MSTAT-C program (Michigan State University v. 2.10). Before running ANOVA, square root transformation was performed in order to ensure normal distribution and homogeneity of variances in germination percentage, germination stress tolerance index and seedling dry weight ratio. Determination of the relations among the characteristics was revealed with correlation analysis by using Minitab version 17 (Minitab Inc., State College, PA, USA), and results were expressed with correlation coefficients [46].

## 3. Results

The effects of flesh color and salt concentrations were found to be statistically significant in all of the characteristics investigated, while plant growth regulators had insignificant effects on germination ratio, shoot length and seedling dry matter ratio. In addition, in some of the traits examined, double or triple interactions of the factors also showed significant effects (Table 1).

**Table 1.** Distribution of germination and emergence performances according to factors.

Flesh Color (FC)	Germination (%)	MGT (Day)	Shoot Length (cm)	Fresh Seedling Weight (mg)	Seedling Dry Matter Ratio (%)	GSTI (%)
White	81.17 ± 24.49 <sup>B</sup>	11.24 ± 5.38 <sup>A</sup>	27.90 ± 9.87 <sup>B</sup>	12.29 ± 3.84 <sup>B</sup>	4.44 ± 1.54 <sup>B</sup>	36.08 ± 39.44 <sup>B</sup>
Red	85.33 ± 13.21 <sup>A</sup>	7.33 ± 3.02 <sup>B</sup>	31.49 ± 10.69 <sup>A</sup>	21.23 ± 7.54 <sup>A</sup>	4.65 ± 1.99 <sup>A</sup>	54.91 ± 34.08 <sup>A</sup>
Salt Concentrations (SC)						
Control	98.44 ± 1.27 <sup>A</sup>	4.74 ± 0.58 <sup>D</sup>	41.56 ± 3.01 <sup>A</sup>	22.85 ± 6.16 <sup>A</sup>	2.87 ± 0.15 <sup>D</sup>	100.0 ± 0.00 <sup>A</sup>
2500 ppm	90.00 ± 6.45 <sup>B</sup>	7.06 ± 1.40 <sup>C</sup>	35.78 ± 3.71 <sup>B</sup>	20.76 ± 6.65 <sup>B</sup>	3.54 ± 0.31 <sup>C</sup>	51.32 ± 18.66 <sup>B</sup>
5000 ppm	89.50 ± 8.23 <sup>B</sup>	9.80 ± 2.40 <sup>B</sup>	26.18 ± 2.65 <sup>C</sup>	14.64 ± 4.06 <sup>C</sup>	4.45 ± 0.41 <sup>B</sup>	25.97 ± 17.67 <sup>C</sup>
10,000 ppm	55.06 ± 18.28 <sup>C</sup>	15.55 ± 4.22 <sup>A</sup>	15.26 ± 1.85 <sup>D</sup>	8.79 ± 1.99 <sup>D</sup>	7.33 ± 0.84 <sup>A</sup>	4.68 ± 4.34 <sup>D</sup>
Plant Growth Regulators (PGRs)						
MC	83.54 ± 19.59	9.16 ± 4.78 <sup>B</sup>	30.09 ± 10.59	16.96 ± 7.73 <sup>A</sup>	4.46 ± 1.70	46.05 ± 37.90 <sup>B</sup>
SA	82.21 ± 22.04	9.62 ± 5.07 <sup>A</sup>	29.37 ± 10.69	16.28 ± 7.25 <sup>B</sup>	4.58 ± 1.77	43.22 ± 38.44 <sup>C</sup>
OA	84.00 ± 17.66	9.08 ± 4.52 <sup>B</sup>	29.63 ± 10.16	17.04 ± 7.51 <sup>A</sup>	4.60 ± 1.88	47.21 ± 38.12 <sup>A</sup>
ANOVA Significance levels						
FC	**	***	***	***	*	***
SC	***	***	***	***	***	***
PGR	ns	*	ns	**	ns	***
FC*SC	***	***	ns	***	***	**
FC*PGR	ns	ns	ns	*	***	***
SC*PGR	*	ns	ns	**	***	***
FC*SC*PGR	ns	ns	ns	**	**	***

\*, \*\*, \*\*\*: Means statistical difference, respectively, at 0.05, 0.01 and 0.001. ns: non-significant. Means followed by different letters within the same columns are significantly different.

Increases in salt concentration slowed the seed germination and caused a decrease in all germination and seedling traits except dry matter content (Table 1). The germination ratio, which had been over 98% in the control, decreased to 55% in the highest saline environment. Simultaneously, mean germination time of seeds extended by 10 days. Additionally, losses in fresh seedling weight (around 6–14 mg) and shoot length (around 10–25 cm) were observed. The drop in GSTI value to 4.7% explains all of these unfavorable impacts, which are presented in Table 1.

Some species/varieties/genotypes can develop resistance or tolerance to certain stress factors through the mechanisms they possess. GSTI, which means seed vigor, was calculated to be much higher (18%) in seeds obtained from red-fleshed fruits. All seed (germination ratio and mean germination time) and seedling (shoot length, fresh seedling weight and seedling dry matter ratio) characteristics investigated obtained from red-fleshed fruits showed significantly better performance, as shown in Table 1.

OA, used as a priming agent, was effective in terms of germination stress tolerance, germination percentage, mean germination time and fresh seedling weight. At the same time, MC was effective regarding seedling length and dry matter accumulation (Table 1).

Findings on the effect of the flesh color of the fruit from which the seed was obtained, varying levels of salt stress and priming agents (SA, OA and MC) on germination percentage and mean germination time of pitaya seeds are given in Table 2. While the germination rate, determined as 98.44% in the control, was not affected much by 2500 ppm (90.00%) and 5000 ppm (89.50%) salt concentrations, it decreased sharply to 55.03% at 10,000 ppm (Table 2). When all the study factors were considered together, the germination percentage (85.33%) of the seeds of the Siam Red was higher than that of Vietnam White (81.16%) (Table 2). In contrast, the mean germination time decreased from 11.24 days in Vietnam White to 7.33 days in Siam Red (Table 2). No statistically significant differences were detected between SA, OA and MC applied for this purpose regarding germination rate and germination speed. At the same time, all three PGRs were observed to make a positive contribution. In both Siam Red (99.33%) and Vietnam White (98.33%) cultivars, SA treatment was prominent in triggering germination under non-stress conditions (Table 2). However, when germination occurred under saline conditions, OA (48.67%) was favored in Vietnam White and MC (72.00%) in Siam Red, and the same was observed for the mean germination time (Table 2). It has been reported that seeds of different species, including pitaya, showed positive effects on germination speed and rate after priming with SA, OA or MC.

**Table 2.** Variation of germination percentage and mean germination time according to factors.

Flesh Color	Salt Concentrations	Germination Percentage (%)			
		MC	SA	OA	Mean
White	0	97.67 ± 1.36	98.33 ± 1.63	98.00 ± 1.26	98.00 ± 1.37 <sup>A</sup>
	2500	94.67 ± 3.27	89.33 ± 5.46	93.33 ± 5.47	92.44 ± 5.11 <sup>A</sup>
	5000	94.67 ± 3.26	92.33 ± 3.20	93.33 ± 4.84	93.44 ± 3.75 <sup>A</sup>
	10,000	39.33 ± 6.89	34.27 ± 14.96	48.67 ± 8.55	40.76 ± 11.79 <sup>B</sup>
	Mean	81.58 ± 25.25	78.57 ± 27.41	83.33 ± 21.20	81.16 ± 24.47 <sup>B</sup>
Red	0	98.67 ± 1.03	99.33 ± 1.03	98.67 ± 1.03	98.89 ± 1.02 <sup>A</sup>
	2500	83.33 ± 7.34	88.67 ± 6.89	90.67 ± 4.84	87.56 ± 6.84 <sup>B</sup>
	5000	88.00 ± 5.66	89.33 ± 8.26	79.33 ± 11.98	85.56 ± 9.61 <sup>B</sup>
	10,000	72.00 ± 10.43	66.00 ± 12.33	69.92 ± 10.79	69.31 ± 10.84 <sup>C</sup>
	Mean	85.50 ± 11.75	85.83 ± 14.62	84.65 ± 13.66	85.33 ± 13.22 <sup>A</sup>
Means of Flesh Colors	0	98.17 ± 1.27 <sup>A</sup>	98.83 ± 1.40 <sup>A</sup>	98.33 ± 1.15 <sup>A</sup>	98.44 ± 1.27 <sup>A</sup>
	2500	89.00 ± 8.02 <sup>A</sup>	89.00 ± 5.94 <sup>A</sup>	92.00 ± 5.12 <sup>A</sup>	90.00 ± 6.45 <sup>B</sup>
	5000	91.33 ± 5.61 <sup>A</sup>	90.83 ± 6.18 <sup>A</sup>	86.33 ± 11.37 <sup>A</sup>	89.50 ± 8.23 <sup>B</sup>
	10,000	55.67 ± 19.03 <sup>AB</sup>	50.14 ± 21.10 <sup>B</sup>	59.29 ± 14.47 <sup>A</sup>	55.03 ± 18.28 <sup>C</sup>
	Mean	83.54 ± 19.59	82.20 ± 22.04	83.99 ± 17.66	83.24 ± 19.71

Table 2. Cont.

Flesh Color	Salt Concentrations	Mean germination time (day)			
		Hormones			
		MC	SA	OA	Mean
White	0	5.31 ± 0.19	5.25 ± 0.19	5.30 ± 0.21	5.29 ± 0.19 <sup>D</sup>
	2500	8.20 ± 0.55	8.79 ± 0.56	7.96 ± 0.20	8.35 ± 0.56 <sup>C</sup>
	5000	11.78 ± 0.72	12.32 ± 0.89	11.90 ± 1.49	12.00 ± 1.05 <sup>B</sup>
	10,000	19.51 ± 1.86	20.10 ± 1.67	18.39 ± 1.34	19.33 ± 1.70 <sup>A</sup>
	Mean	11.22 ± 5.50	11.61 ± 5.69	10.89 ± 5.12	11.24 ± 5.38 <sup>A</sup>
Red	0	4.20 ± 0.23	4.25 ± 0.21	4.15 ± 0.10	4.20 ± 0.18 <sup>D</sup>
	2500	5.73 ± 0.43	6.11 ± 0.27	5.46 ± 0.42	5.77 ± 0.46 <sup>C</sup>
	5000	7.18 ± 0.54	7.54 ± 0.65	8.06 ± 0.54	7.59 ± 0.66 <sup>B</sup>
	10,000	11.28 ± 0.57	12.56 ± 2.88	11.46 ± 1.43	11.77 ± 1.87 <sup>A</sup>
	Mean	7.10 ± 2.72	7.62 ± 3.44	7.28 ± 2.95	7.33 ± 3.02 <sup>B</sup>
Means of Flesh Colors	0	4.75 ± 0.61	4.75 ± 0.56	4.72 ± 0.62	4.74 ± 0.58 <sup>D</sup>
	2500	7.02 ± 1.42	7.45 ± 1.46	6.71 ± 1.34	7.06 ± 1.40 <sup>C</sup>
	5000	9.48 ± 2.48	9.93 ± 2.60	9.98 ± 2.27	9.78 ± 2.40 <sup>B</sup>
	10,000	15.40 ± 4.49	16.33 ± 4.53	14.92 ± 3.85	15.55 ± 4.22 <sup>A</sup>
	Mean	9.16 ± 4.77 <sup>B</sup>	9.62 ± 5.07 <sup>A</sup>	9.08 ± 4.51 <sup>B</sup>	9.29 ± 4.77

Means followed by different letters within the same columns and rows are significantly different.

The results of how the shoot length, fresh seedling weight and seedling dry weight ratio of the seedlings were affected by the combined effect of the factors are given in Table 3. According to the results, regardless of the treatments, an increase in seedling dry matter content and decreases in shoot length and fresh seedling weight were observed in parallel with the increase in salt concentration. At the same time, the values varied between 2.87–7.34%, 15.26–41.56 mm and 8.78–22.85 mg, respectively (Table 3).

Shoot length, fresh seedling weight and seedling dry matter content, which are defined as seedling development and quality criteria, were higher in Siam Red (31.48 mm, 21.23 mg and 4.65%, respectively) than in Vietnam White (27.90 mm, 12.23 mg and 4.44%, respectively) (Table 3), suggesting that *H. polyrhizus* is more tolerant to salt stress.

Table 3. Variation of shoot length and fresh seedling weight and seedling dry matter ratio according to factors.

Flesh Color	Salt Concentrations	Shoot Length (mm)			
		Plant Growth Regulator			
		MC	SA	OA	Mean
White	0	39.83 ± 3.31	38.83 ± 2.56	41.00 ± 2.00	39.89 ± 2.68 <sup>A</sup>
	2500	33.00 ± 1.05	31.92 ± 1.53	33.92 ± 1.20	32.94 ± 1.46 <sup>B</sup>
	5000	25.00 ± 1.26	25.17 ± 2.06	24.00 ± 2.09	24.72 ± 1.82 <sup>C</sup>
	10,000	14.67 ± 1.17	13.33 ± 1.57	14.17 ± 1.13	14.06 ± 1.35 <sup>D</sup>
	Mean	28.12 ± 9.75	27.31 ± 9.78	28.27 ± 10.47	27.90 ± 9.87 <sup>B</sup>
Red	0	43.67 ± 2.50	43.83 ± 2.64	42.17 ± 1.94	43.22 ± 2.37 <sup>A</sup>
	2500	39.75 ± 1.44	39.75 ± 2.16	36.33 ± 3.92	38.61 ± 3.04 <sup>B</sup>
	5000	29.08 ± 2.31	25.50 ± 2.49	28.33 ± 1.54	27.64 ± 2.57 <sup>C</sup>
	10,000	15.75 ± 2.02	16.58 ± 0.74	17.08 ± 1.24	16.47 ± 1.46 <sup>D</sup>
	Mean	32.06 ± 11.23	31.42 ± 11.35	30.98 ± 9.87	31.48 ± 10.69 <sup>A</sup>
Means of Flesh Colors	0	41.75 ± 3.44	41.33 ± 3.60	41.58 ± 1.97	41.56 ± 3.01 <sup>A</sup>
	2500	36.37 ± 3.72	35.83 ± 4.46	35.12 ± 3.04	35.78 ± 3.71 <sup>B</sup>
	5000	27.04 ± 2.78	25.33 ± 2.19	26.17 ± 2.86	26.18 ± 2.65 <sup>C</sup>
	10,000	15.21 ± 1.67	14.96 ± 2.06	15.62 ± 1.89	15.26 ± 1.85 <sup>D</sup>
	Mean	30.09 ± 10.59	29.36 ± 10.68	29.62 ± 10.16	29.69 ± 10.41

Table 3. Cont.

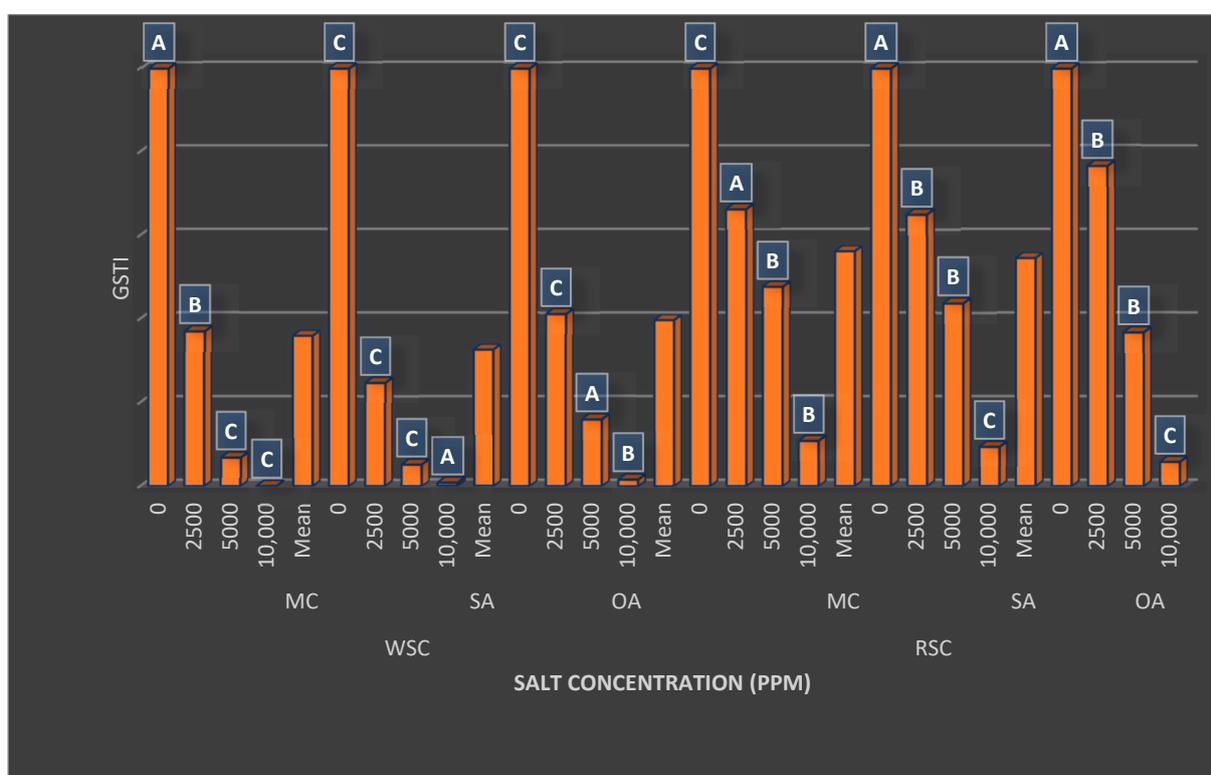
Fresh seedling weight (mg)					
Flesh Color	Salt Concentrations	Plant Growth Regulator			
		MC	SA	OA	Mean
White	0	16.89 ± 1.01 <sup>BC</sup>	16.50 ± 0.95 <sup>BC</sup>	17.06 ± 0.74 <sup>BC</sup>	16.82 ± 0.89 <sup>A</sup>
	2500	14.71 ± 1.13 <sup>C</sup>	14.18 ± 0.08 <sup>C</sup>	14.48 ± 1.07 <sup>C</sup>	14.45 ± 0.87 <sup>B</sup>
	5000	11.39 ± 0.45 <sup>CD</sup>	10.97 ± 1.06 <sup>CD</sup>	10.51 ± 0.93 <sup>CD</sup>	10.96 ± 0.89 <sup>C</sup>
	10,000	7.07 ± 0.25 <sup>D</sup>	6.71 ± 0.31 <sup>D</sup>	6.97 ± 0.22 <sup>D</sup>	6.92 ± 0.29 <sup>D</sup>
	Mean	12.51 ± 3.86 <sup>A</sup>	12.09 ± 3.81 <sup>A</sup>	12.25 ± 3.99 <sup>A</sup>	12.29 ± 3.83 <sup>B</sup>
Red	0	28.94 ± 0.55 <sup>A</sup>	29.03 ± 0.54 <sup>A</sup>	28.69 ± 0.40 <sup>A</sup>	28.89 ± 0.49 <sup>A</sup>
	2500	28.28 ± 0.23 <sup>A</sup>	25.58 ± 3.14 <sup>AB</sup>	27.36 ± 2.41 <sup>A</sup>	27.07 ± 2.44 <sup>B</sup>
	5000	18.89 ± 1.41 <sup>B</sup>	16.14 ± 1.43 <sup>B</sup>	19.92 ± 1.38 <sup>B</sup>	18.32 ± 2.11 <sup>C</sup>
	10,000	9.53 ± 0.45 <sup>CD</sup>	11.11 ± 0.09 <sup>CD</sup>	11.31 ± 0.22 <sup>CD</sup>	10.65 ± 0.86 <sup>D</sup>
	Mean	21.41 ± 8.13 <sup>A</sup>	20.46 ± 7.50 <sup>B</sup>	21.82 ± 7.19 <sup>A</sup>	21.23 ± 7.54 <sup>A</sup>
Means of Flesh Colors	0	22.92 ± 6.34 <sup>A</sup>	22.76 ± 6.58 <sup>A</sup>	22.87 ± 6.10 <sup>A</sup>	22.85 ± 6.16 <sup>A</sup>
	2500	21.50 ± 7.13 <sup>A</sup>	19.88 ± 6.32 <sup>B</sup>	20.92 ± 6.96 <sup>A</sup>	20.76 ± 6.65 <sup>B</sup>
	5000	15.14 ± 4.04 <sup>C</sup>	13.56 ± 2.95 <sup>BC</sup>	15.21 ± 5.04 <sup>C</sup>	14.64 ± 4.06 <sup>C</sup>
	10,000	8.30 ± 1.33 <sup>D</sup>	8.91 ± 2.31 <sup>D</sup>	9.14 ± 2.27 <sup>D</sup>	8.78 ± 1.99 <sup>D</sup>
	Mean	16.96 ± 7.74 <sup>A</sup>	16.28 ± 7.25 <sup>B</sup>	17.04 ± 7.52 <sup>A</sup>	16.76 ± 7.46
Seedling dry matter ratio (%)					
Flesh Color	Salt Concentrations	Plant Growth Regulator			
		MC	SA	OA	Mean
White	0	2.99 ± 0.06 <sup>C</sup>	3.01 ± 0.05 <sup>C</sup>	2.97 ± 0.04 <sup>C</sup>	2.99 ± 0.05 <sup>D</sup>
	2500	3.46 ± 0.15 <sup>BC</sup>	3.66 ± 0.15 <sup>BC</sup>	3.78 ± 0.07 <sup>BC</sup>	3.64 ± 0.18 <sup>C</sup>
	5000	4.51 ± 0.07 <sup>B</sup>	4.39 ± 0.19 <sup>B</sup>	3.90 ± 0.48 <sup>BC</sup>	4.27 ± 0.39 <sup>B</sup>
	10,000	7.06 ± 0.17 <sup>A</sup>	7.37 ± 0.36 <sup>A</sup>	6.19 ± 0.87 <sup>A</sup>	6.88 ± 0.73 <sup>A</sup>
	Mean	4.51 ± 1.61 <sup>A</sup>	4.61 ± 1.71 <sup>A</sup>	4.21 ± 1.31 <sup>B</sup>	4.44 ± 1.54 <sup>B</sup>
Red	0	2.76 ± 0.12 <sup>C</sup>	2.77 ± 0.13 <sup>C</sup>	2.69 ± 0.09 <sup>C</sup>	2.74 ± 0.11 <sup>D</sup>
	2500	3.10 ± 0.11 <sup>BC</sup>	3.48 ± 0.35 <sup>BC</sup>	3.76 ± 0.28 <sup>BC</sup>	3.45 ± 0.38 <sup>C</sup>
	5000	4.90 ± 0.30 <sup>B</sup>	4.54 ± 0.43 <sup>B</sup>	4.46 ± 0.08 <sup>B</sup>	4.63 ± 0.35 <sup>B</sup>
	10,000	8.00 ± 0.70 <sup>A</sup>	7.43 ± 0.78 <sup>A</sup>	7.92 ± 0.54 <sup>A</sup>	7.78 ± 0.69 <sup>A</sup>
	Mean	4.69 ± 2.15 <sup>A</sup>	4.56 ± 1.87 <sup>A</sup>	4.71 ± 2.02 <sup>A</sup>	4.65 ± 1.99 <sup>A</sup>
Means of Flesh Colors	0	2.88 ± 0.15 <sup>B</sup>	2.89 ± 0.16 <sup>B</sup>	2.83 ± 0.16 <sup>B</sup>	2.87 ± 0.15 <sup>D</sup>
	2500	3.28 ± 0.23 <sup>B</sup>	3.57 ± 0.27 <sup>AB</sup>	3.77 ± 0.19 <sup>AB</sup>	3.54 ± 0.31 <sup>C</sup>
	5000	4.71 ± 0.29 <sup>AB</sup>	4.47 ± 0.33 <sup>AB</sup>	4.18 ± 0.44 <sup>AB</sup>	4.45 ± 0.41 <sup>B</sup>
	10,000	7.53 ± 0.69 <sup>A</sup>	7.40 ± 0.58 <sup>A</sup>	7.06 ± 1.14 <sup>A</sup>	7.34 ± 0.84 <sup>A</sup>
	Mean	4.46 ± 1.70	4.58 ± 1.77	4.60 ± 1.88	4.55 ± 1.78

Means followed by different letters within the same columns and rows are significantly different.

When factor effects were analyzed together, there was no difference between PGRs in terms of shoot length and seedling dry matter content, while OA (17.04 mg) and MC (16.96 mg) were more effective than SA (16.28 mg) in terms of fresh seedling weight (Table 3). At the highest salt stress dose of 10,000 ppm, OA was found to be the highest in shoot length (15.62 mm), fresh seedling weight (9.14 mg) and seedling dry matter content (4.60%) (Table 3).

The results of the stress tolerance index, which is the cumulative effect of the traits summarized above, detailed according to the factors, are given in Figure 1. When the effect of other factors is ignored, the increase in salt concentration causes the stress tolerance index to decrease, which was also reported by [45,47]. However, the fact that seeds obtained from fruits with red fruit flesh were more resistant to salinity-induced stress can be interpreted as the effect of the maternal environment. The maternal environment, defined as the maternal parent effects other than gene effects, has shown significant effects on resistance to different biotic and abiotic stress conditions [10,48]. Considering the fact that saline and

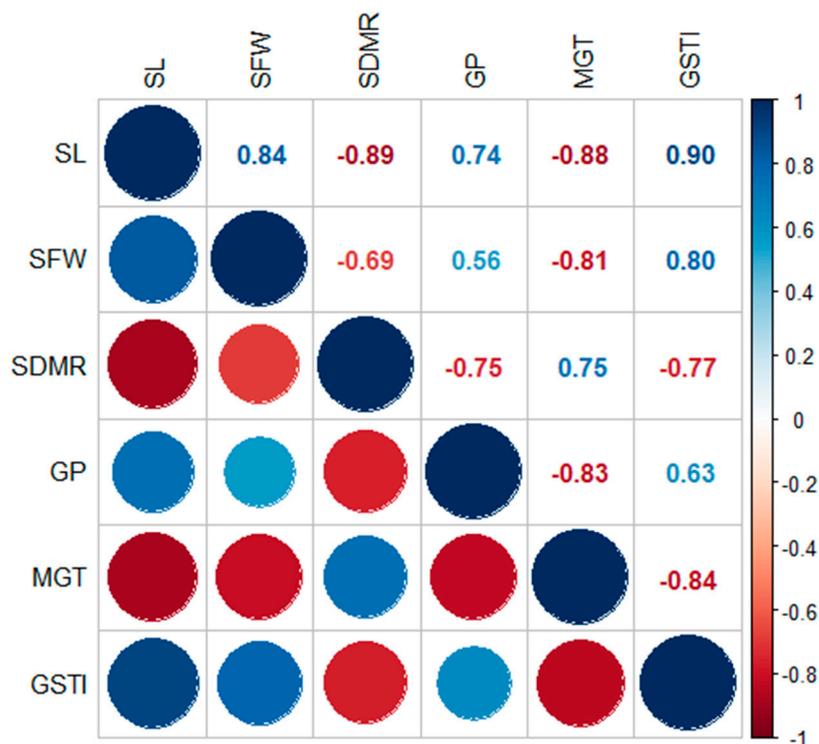
arid areas will increase under the current global climate change, *H. polyrhizus* cultivars may be promising as parents in hybridizations in order to develop stress-resistant genotypes with superior fruit characteristics such as high antioxidant activity due to their diverse and higher phytochemicals [49], in addition to their resistance [16]. It was observed that all PGRs applied as priming agents were effective in reducing stress conditions, but they were ranked as OA > MC > SA. However, the interactions of the factors on the stress tolerance index were found to be significant. According to the results, MC was more effective as a priming agent in seeds obtained from fruits with white fruit flesh, while a similar effect was found in seeds with red fruit flesh due to OA treatment (Figure 1). Until new salt-tolerant genotypes are developed, identification of species-specific priming agents in the short term for saline environments is crucial in terms of contributing to research and cultivation of pitaya. SA, OA and MC are widely used to alleviate the negative effects caused by different stress conditions [34–36,40,41].



**Figure 1.** Variation of germination stress tolerance index according to factors (LSD (%): Seed C: 0.51, Salt C: 0.69, Horm: 0.64, Seed CxSalt C: 0.98, Seed CxHorm: 0.96, Salt CxHorm: 1.20, Seed CxSalt CxHorm: 1.70, F Values (%): Seed C: 3223.38, Salt C: 30,224.38, Horm: 521.50, Seed CxSalt C: 1458.50, Seed CxHorm: 193.87, Salt CxHorm: 48.00, Seed CxSalt CxHorm: 30.80, Means followed by different letters on different bars are significantly different.).

The results of the relations between the traits examined in the study are given in Figure 2. Since the development in the plumule leads to an increase in biomass, there was a high positive correlation between seedling length and fresh seedling weight ( $r: 0.84$ ). However, since the development in tissues caused an increase in intercellular spaces, a high negative correlation was found between shoot length and seedling dry matter content ( $r: -0.89$ ). It is known that an increase in intercellular spaces leads to a decrease in the amount of dry matter accumulated per unit area [50]. Mean germination time is one of the important criteria for determining seed strength. If the time is prolonged, a decrease in germination rate and developmental retardation in germinated seedlings are observed [45]. The results of the study were in this direction, and strong negative relationships were found between mean germination time and germination percentage ( $r: -0.83$ ), seedling length

( $r$ :  $-0.88$ ) and fresh seedling weight ( $r$ :  $-0.81$ ). Conversely, the increase in germination stress tolerance positively affected shoot length ( $r$ :  $0.90$ ), fresh seedling weight ( $r$ :  $0.80$ ) and germination percentage ( $r$ :  $0.63$ ), which are expressed as quality seed parameters, while shortening the mean germination time ( $r$ :  $-0.84$ ). However, a negative correlation ( $r$ :  $-0.77$ ) was calculated between GSTI and seedling dry matter ratio due to the increase in intercellular space in seedlings with vigorous growth. Germination percentage, which is one of the most important parameters determining seed quality, contributed to the increase in the stress tolerance index ( $r$ :  $0.63$ ) and plant biomass ( $r$ :  $0.56$ ) while decreasing the mean germination time ( $r$ :  $-0.84$ ). The results are consistent with previous studies [45,51].



**Figure 2.** Correlations among investigated characteristics (SL: Seedling length, SFW: Seedling fresh weight, SDMR: Seedling dry matter ratio, GP: Germination percentage, MGT: Mean germination time, GSTI: Germination stress tolerance index).

#### 4. Discussion

Agricultural production depends on the suitability of ecological factors, and sometimes it is necessary to cultivate under different stress conditions [52]. In these cases, it can be critical to know the tolerance of the material to the prevailing stress conditions or the practices to counteract this stress [53]. Due to water deficiency (osmotic stress), ion toxicity, and ion imbalance (ionic stress), or a combination of these factors [54,55], high salinity levels have an adverse effect on seed germination and plant growth, ultimately inhibiting germination and preventing crop production. Because of the low osmotic potential caused by high soil salinity, which hinders water uptake by the seed, seed germination is typically inhibited [56]. In addition, excessive soil salt and chloride ion concentrations may be hazardous to seeds [57].

An increase in salt concentration increases the osmotic pressure of the seed and inhibits water uptake. Due to the lower water flux caused by the osmotic effect, salt stress affects seed metabolism and can lead to the inhibition of reserve mobilization [58]. Disruption of ion balance and increased reactive oxygen species lead to cell integrity and homeostasis disruption; the latter acts on different chemical components of the seed, disrupting the metabolic cycle. All these conditions lead to loss of seed viability or reduced performance [19–22]. The study findings were similar to those of the previous studies. In

parallel with the increase in salt concentration, there was a decrease in the germination rate and an increase in the mean germination time. There are reports of decreased seed germination at increasing salt concentrations in different species such as cotton [41] and cucumber [47], including pitaya [18]. Ascending salt concentrations not only prevent seed germination but also extend the germination time by delaying the start of germination [59].

Increased salt concentration in the seed interferes with the conversion of macromolecules, which are a source for respiration, limiting the formation of soluble sugars necessary for embryo development. This disruption of the energy flow causes germination not to occur at all, to stop at a certain stage or to retard development [19,20,25]. Based on these reasons, shoot length and fresh seedling weight, which are defined as seedling development and quality criteria, were also decreased under saline conditions. Our results are in agreement with other reports conducted on different species, such as sunflower [59], sugar beet [51] and pitaya [16].

Genotypes show high variation in salt tolerance through different adaptation pathways. In studies examining pitaya varieties with different flesh colors, the juices of varieties with red flesh color were found to have higher values in terms of pH and antioxidant activity [60,61]. Pitaya seeds with red fruit flesh have higher oil and sugar reserves [61]. Betalain derivatives, a natural osmolyte and antioxidant, K, which has a high ion exchange potential with Na, hydrolytic enzymes that catalyze metabolic events and antioxidants that eliminate the negative effects caused by excessive ROS are found at higher levels in *H. polyrhizus* with red fruit flesh [49,62,63].

The better performance of the Siam Red under saline conditions may be because its seeds are realized in a halophytic environment from the formation and development stage. Indeed, in *Anabasis setifera*, the maternal environment has been proven to affect resistance to salt stress significantly [48]. In addition, the high level of antioxidant activity may have contributed to lower negative effects caused by ROS. Seeds of different pitaya species were germinated under salt stress [16], and a 33% decrease in the germination rate of *H. undatus* with white fruit flesh was observed, while no decrease was reported in *H. polyrhizus* with red fruit flesh. Similarly, the reduction in the germination rate of seeds from white fruit flesh (62%) was higher than in that of red (46%). In conclusion, it was emphasized that *H. polyrhizus* is more tolerant to salt stress than *H. undatus*, which is similar to the results of the current study.

The cumulative effect of both seed composition and maternal environment factors that favor tolerance to salt stress allowed for better results in *H. polyrhizus* seedlings growing under salt stress.

Seeds that have been primed before being sown have improved imbibition capability, pre-germinative metabolic processes, seedling emergence, growth, vigor, productivity, and salinity adaptation. To maintain genome integrity, seed priming improves DNA repair, stabilizes RNA, and boosts new protein synthesis. Priming practices may allow sustainable cultivation in areas where soil or irrigation water has high salinity before sowing. In these areas where ecological factors are unsuitable, it is vital to determine species-specific priming agents [25,45]. Using PGRs that regulate different physiological events can successfully alleviate stress effects [64,65]. These positive effects have been proven to be because these chemicals act as signaling agents, maintain ion homeostasis, maintain membrane stability, suppress ROS and are involved in different physiological process [25–28,33].

The prominence of OA, an important osmoregulatory and antioxidant known to be positively correlated with K availability in stress conditions [66], may be interpreted as the seed trying to maintain ion homeostasis primarily to relieve salt stress. In the remediation of different heavy metals, exogenous application of OA to plants increased tolerance, enabling higher levels of heavy metal accumulation. In addition, among the grapevine rootstocks, it was emphasized that the genotype with the highest resistance to Na stress was the one containing the highest level of OA, and it was reported to show significant effects in eliminating Na stress [67].

## 5. Conclusions

Nowadays, priming techniques, which are used especially by commercial seed companies with coating technology, is widely used against stress factors such as salinity. This study investigated the effect of some plant growth regulators as priming agent and maternal environment as a first report on the performance of seeds obtained from pitaya fruits with different fruit flesh colors under different salt stress conditions during germination and seedling emergence periods. According to the results, it was determined that the environment in which the seed was grown was important in salt stress resistance, while seeds matured in the environment from red fruit flesh were more tolerant to salt stress than seeds from white fruit flesh. Although pitaya species are relatively salt-tolerant, growth of seedlings was significantly reduced above 2500 ppm and germination percentage started to decrease at 5000 ppm. In reducing the stress caused by NaCl, MC can be used as a priming agent in seeds obtained from fruits with white fruit flesh, and OA can be used as a priming agent in seeds obtained from fruits with red fruit flesh. It is planned to expand the scope of the study by increasing the number of species and cultivars. If the maternal effect is found to be significant still, reciprocal hybridizations will be planned in order to reveal the inheritance pattern of salt resistance and obtain new genotypes with resistance and superior fruit characteristics. It is thought that all the results obtained and that will be obtained could contribute to the cultivation and breeding of pitaya.

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