



Article Effect of Salinity and Temperature on the Seed Germination and Seedling Growth of Desert Forage Grass Lasiurus scindicus Henr.

Jahangir A. Malik ¹, AbdulAziz A. AlQarawi ¹, Mashail N. AlZain ²,*, Basharat A. Dar ¹, Muhammad M. Habib ¹ and Salah Nasser S. Ibrahim ¹

- ¹ Plant Production Department, College of Food and Agricultural Sciences, King Saud University, P.O. Box 2460, Riyadh 11451, Saudi Arabia; jmalik@ksu.edu.sa (J.A.M.); alqarawi@ksu.edu.sa (A.A.A.); bdar@ksu.edu.sa (B.A.D.); mhabib@ksu.edu.sa (M.M.H.); salahsar2008@gmail.com (S.N.S.I.)
- ² Department of Biology, College of Sciences, Princess Nourah Bint Abdulrahman University, P.O. Box 84428, Riyadh 11451, Saudi Arabia
- * Correspondence: mnalzain@pnu.edu.sa

Abstract: Lasiurus scindicus Henr. is one of the most important forage grass species of the Arabian deserts. Temperature and soil salinity are well known to influence the germination and seedling development of various forage species. Therefore, in the current study, the effect of temperature and salinity and their interaction on the germination parameters, seedling growth, and physiological parameters of L. scindicus were evaluated. For this reason, L. scindicus seeds were treated with five salinity concentrations (i.e., 0, 50, 100, 150, and 200 mM NaCl) and incubated at two temperature levels (T1 = 25/20 °C, D/N and T2 = 35/30 °C, D/N). The results indicated that the salinity and temperature significantly affected the germination indices, seedling growth parameters, chlorophyll, and proline content. The highest germination percentage (GP; 90%) was recorded in the non-salinetreated seeds incubated at T1. The seeds at T2 under the non-saline treatment exhibited an increased germination rate (GR = 17.5%). The interactive effect of salinity and temperature on germination and growth parameters was significant, indicating that the germination response to salinity depends on temperature. The germination of seeds treated with 200 mM NaCl was completely inhibited at both temperatures T1 and T2. However, the ungerminated seeds at both T1 (85%) and T2 (78%) restored their germination abilities after they were transferred to distilled water. Also, the seed vigor index (SVI) constantly showed a decline with the increasing salinity levels especially at T2, which was lowest when seeds were treated with 150 mM salinity. Growth parameters (i.e., aRL, aSL, RDW, SDW, SB, and SLA) and the chlorophyll content showed a similar pattern as that of germination. However, the proline content (shoot proline and root proline) showed a progressive increase with increasing salinity and temperature. All of these characteristics indicate that L. scindicus seeds were not able to germinate under extreme salinity and temperature conditions but remained viable in a state of enforced dormancy. This is most likely an important adaptive strategy of this species for survival in the high-saline changing habitats of the arid region of Saudi Arabia, and thus, it can be an excellent choice for restoring degraded rangelands and salinity-inflicted abundant farmlands for forage agriculture.

Keywords: Lasiurus scindicus; salinity; temperature; seed germination; chlorophyll; proline; restoration

1. Introduction

Seed germination is a fundamental physiological process in the successful growth and development of plants [1,2], and is significantly affected by temperature, soil salinity, etc. [3,4]. The germination and seedling phases in the plant life cycle are the most vulnerable to extreme environmental stressors, especially for desert plants [5,6].



Citation: Malik, J.A.; AlQarawi, A.A.; AlZain, M.N.; Dar, B.A.; Habib, M.M.; Ibrahim, S.N.S. Effect of Salinity and Temperature on the Seed Germination and Seedling Growth of Desert Forage Grass *Lasiurus scindicus* Henr. *Sustainability* **2022**, *14*, 8387. https://doi.org/10.3390/su14148387

Academic Editor: Sara Magrini

Received: 22 April 2022 Accepted: 5 July 2022 Published: 8 July 2022

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.



Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Salinity is one of the most significant abiotic stresses impacting plant growth and development worldwide [7,8]. It is a primary cause of soil degradation and has a detrimental impact on ecological restoration and rebuilding in desert regions [9,10]. Salinity is prevalent in arid regions and impacts seed germination and its subsequent phases such as seedling establishment and growth [11,12]. Soil is saline when the electrical conductivity (EC) of its saturation extract (ECe) at the root zone exceeds 4 dS/m [13]. According to various reports, salt stress affects about a billion hectares of land globally [8,14]. Furthermore, for a variety of causes, which include high surface evaporation and inadequate amounts of precipitation, weathering of native rocks, irrigation with saline water, and poor cultural practices, salinized areas continue to increase in size at a pace of 10% annually, especially in arid and semiarid regions [7,15]. By the year 2050, it is anticipated that more than half of all arable land will be salinized [7,8,16].

Salinity stress disrupts enzymes and other biological functions, causing ionic leakage from cell membranes and hence cell malfunction [8,17]. It also induces inhibition of the chlorophyll biosynthesis pathway, thus, decreasing plant photosynthesis [18,19]. Furthermore, salinity damages plant functioning and growth by reducing water uptake capacity, weakening root structure, causing ionic toxicity, and osmotic stress [20]. All of these factors influence seed germination percentages and rates, as well as root and shoot length, and dry weight [8,21]. Salt stress has also been reported to increase proline content as a protective mechanism [22].

The influence and importance of temperature on seed quality and germination have long been acknowledged [23,24]. It is considered one of the most prominent environmental factors regulating growth and development by altering all individual reactions and stages of germination in a plant [25–27]. Extreme warming, for example, is predicted to become more common in the future [28–30]. Seed germination could be harmed as a result of such a shift [31,32]. Also, global warming generally increases surface evaporation, encouraging soil salinization and making it more problematic [33]. As a result, salinity and temperature, especially in dry and semiarid regions, would have a combined effect on seed germination, seedling growth, chlorophyll content, and proline accumulation [34,35]. For example, all plant species have an ideal temperature for seed germination, which allows seeds to germinate more effectively than at other temperatures [36]. Also, at optimum temperatures, as in the previous studies, the salinity tolerance of plants was higher, and any fluctuation in temperature hindered germination at all salinities [37,38]. Thus, it becomes critical to investigate the combined impact of salinity and temperature on the germination and viability of desert plants, which will increase knowledge for understanding plants' tolerance to salinity under fluctuating temperatures at the germination and seedling stage [39,40].

Through different mechanisms, seeds have developed the ability to delay germination and survive under high stresses until the arrival of favorable conditions through subsequent environmental events [36,41]. The germination recovery test is frequently used to evaluate if salt stress damaged seeds or just prevented them from germinating [41]. Although the majority of the literature suggests that halophytes have better germination recovery than glycophytes, a few studies have looked at germination recovery in glycophytes [11,42]. Grasses resist salinity stress differently at the germination stage than halophytes, which usually have a lower tolerance.

Lasiurus scindicus Henrard (*Poaceae*) is a perennial, multibranched, C₄ desert grass. It is a drought-resilient plant and can grow well in areas where annual precipitation is around 200 mm [43]. It is naturally distributed in the dry regions of Africa, Asia, and Saudi Arabia [43–45]. It is nutritiously valuable forage, mainly for ruminants, and grows well on sandy plains, low sand dunes, hummocks [44,46], and occasionally in the coastal habitats of the Arabian Peninsula [47]. This plant is a moderately salt-tolerant species that plays an important role in rangeland stability [8,48,49]. All these traits make *L. scindicus* a competent candidate for the restoration of degraded ranges.

The previous studies reported that increasing salinities under various temperatures had a negative effect on the germination and growth of the *L. scindicus* plant [8,42]. No

such work is reported from the rangelands of Saudi Arabia. Therefore, the goal of this study was to evaluate how well *L. scindicus* seeds tolerate various salinity levels under fluctuating temperatures in a controlled laboratory experiment. Also, the ability of the seeds to recover germination capacity when transferred from saline solutions to distilled water was investigated. This would provide a crucial framework and understanding for the restoration of salinity-inflicted deserts through the cultivation of *L. scindicus* plants. We hypothesized that (1) seed germination would consistently decrease with increasing salinity, (2) the germination at the optimum temperature (the temperature at which *L. scindicus* grows naturally) will be highest at all salinity levels, and (3) the ungerminated seeds will recover their ability to germinate once transferred to distilled water.

2. Materials and Methods

2.1. Collection of Lasiurus scindicus Seeds

Spikes with developed seeds of *Lasiurus scindicus* were collected from the natural population grown in the escarpment habitat of Thumamah National Park, Riyadh, Saudi Arabia. Thumamah National Park is a natural habitat located around 100 km north of Riyadh, Saudi Arabia's capital. The park is a huge and shallow depression with an average yearly precipitation of less than 20 mm. The average yearly temperature in the area ranges from 18 °C in the winter to 37 °C in the summer (Table 1) [50]. Also, the climate data of the Riyadh region were collected between 1999 and 2019 from https://en.climate-data. org/asia/saudi-arabia-29/ (accessed on 15 November 2021; Supplementary Figure S1). The different plant types associated with *L. scindicus* in the escarpment habitat of this park were Panicum turgidum, Haloxylon salicornicum, Cenchrus ciliaris, Rhanterium epapposum, and Acacia ehrenbergiana. The collected spikes were air-dried at room temperature (20–25 °C) in the Range Science Lab, College of Food Science and Agriculture, King Saud University, Riyadh, Saudi Arabia. The seeds from the air-dried spikes were separated by manual handpicking and stored in air-tight containers at room temperature (20–25 $^{\circ}$ C) with 16% humidity for a period of four months, until further experimentation. These stored seeds were later surface sterilized for 3 min in a 5% sodium hypochlorite (NaClO) solution. The seeds were rinsed thrice with sterilized distilled water to remove the solution prior to 1 h of drying at room temperature. The seed health/quality was tested by germinating 100 seeds in moistened Petri plates with distilled water at room temperature, replicated thrice, and found to be $\approx 100\%$. The seeds were later used for the germination experiment under two temperatures and five levels of salinity.

Table 1. Seed collection site and its characteristics.

Species	Country	Site	Location	Seed Color	Seed Weight
Lasiurus scindicus	Saudi Arabia	Escarpment habitats of Thumamah National Park, Riyadh	25°08′13.7″ N 46°36′00.9″ E	Dark Brown	4.02 ± 0.1494 g/ 1000 seeds

2.2. Gemination Experiment

A controlled Petri plate germination experiment [51] on the seeds of *L. scindicus* was conducted using two factors (temperature and salinity). The experiment was conducted at the Plant Production Department, College of Food and Agricultural Sciences, King Saud University, Riyadh. Two temperatures (i.e., 25/20 °C, D/N = T1 and 35/30 °C, D/N = T2) were used to imitate the habitat temperature conditions for spring and late summer for the Riyadh region, Saudi Arabia [50], when the plant produces fully mature seeds. Also, five salinity levels (i.e., 0 mM NaCl concentration (Control), 50, 100, 150, and 200 mM NaCl) were applied to study the salt tolerance level of the seeds under these two temperatures. A total of five replicates with twenty seeds for each treatment were used. All the seeds were evenly arranged in the sterilized plastic Petri dishes (\emptyset : 9 cm) lined with double sterilized Whatman No. 1 filter paper. Saline solutions (5 mL/Petri) were applied and the Petri

dishes were sealed in zipping lock plastic bags to avoid any moisture loss by evaporation. Two incubators (LEEC PL33 Plant Growth and Seed Germination Cabinet, LEEC Limited, Nottingham, UK), each set at the two applied temperatures and a 12/12 hours' light/dark photoperiod were used. A total of 50 Petri dishes (2 temperature \times 5 salinity \times 5 replicates) were randomly placed in the two incubators.

The germination readings were carried out on daily basis throughout the experimentation. The seed was considered to be germinated only when the radicle length reached 2 mm. After twenty days of incubation, the germination counts were stopped. The germination parameters assessed were germination percent (GP), germination rate (GR), seed vigor index (SVI), cumulative germination speed, and recovery germination percent. The values of GP, GR, and SVI were calculated as per the following equations:

 $Germination(\%) = \frac{\textit{total number of seeds germinated}}{\textit{total number of seeds in petri}} \times 100$

Germination rate =
$$\sum \frac{X_{i}}{Y_{i}}$$

where Xi is the number of germinated seeds and Yi is the day corresponding to Xi [52].

$$SVI = (SL + RL) \times GP$$

where SL = shoot length, RL = root length, and GP = germination percentage.

It is worth noting that at the 200 mM salinity treatment, seeds from both incubating temperatures (T1 and T2) showed no germination.

2.3. Measurement of Growth Parameters

At the end of the germination period, five seedlings were randomly selected from each Petri dish to measure the growth parameters. The shoot (aSL = average shoot length (n = 5), SDW = shoot dry weight, and SLA = specific leaf area) and root (aRL = average root length (n = 5), RDW = root dry weight) traits were calculated. The SLA was calculated based on leaf weight and leaf area (scanned and calculated by using WIN 2.0 software). Also, the overall seedling biomass (SIB) was calculated after oven drying the whole seedlings at 70 °C for 72 h.

2.4. Chlorophyll Estimation

Chlorophyll *a*, chlorophyll *b*, and total chlorophyll were obtained by mashing 100 mg of seedling tissue in 10 mL 80% acetone solution [53]. The homogenate was centrifuged at 5000 rpm for 5 min using a Benchtop Centrifuge-5810R, Eppendorf, Hamburg, Germany. The samples were then incubated in the dark for three hours before the absorbance at wavelengths 645 and 663 were measured using a UV–VIS spectrophotometer (SHIMADZU, Kyoto, Japan, UV1800).

2.5. Estimation of Proline Content

Proline ($\mu g/gFW$) for the shoot and root of the *L. scindicus* seedlings was calculated by homogenizing 100 mg of fresh plant shoot and root tissue in 10 mL of sulfosalicylic acid (3%) with a mortar and pestle. The homogenate was centrifuged at 5000 rpm for 10 min (Benchtop Centrifuge-5810R, Eppendorf, Hamburg, Germany), and 2 mL of supernatant was extracted in a separate test tube. The extract (2 mL) was incubated for 1 h in a boiling water bath (at 94–100 °C) with glacial acetic acid and ninhydrin (2 mL each), followed by an ice shock. To this, 4 mL of toluene was added, and the toluene-containing chromophore was collected in a separate tube after mixing for 20 s. The absorbance was measured at 520 nm using a UV–VIS spectrophotometer (SHIMADZU, Kyoto, Japan, UV1800) [54]. A standard curve was obtained using known concentrations of proline.

2.6. Data Analysis

The experiment was conducted as a factorial completely randomized design (CRD) with five replicates for each treatment. The experiment was repeated twice to avoid any experimental error, and before performing statistical analysis, data from both the experiments were averaged. The data generated in the experiment were analyzed using the statistical package Statistics version 8.1 and SAS 9.2 (Oliver Schabenberger, SAS Institute Inc., Cary, NA, USA). The data were subjected to a two-way analysis of variance (ANOVA) to evaluate the effect of two main factors (temperature and salinity) and their interaction on the germination parameters, seedling growth, and recovery germination percentage. Prior to statistical analysis, germination percentage data were arcsine transformed so that the homogeneity of variance was ensured. However, untransformed data are presented in figures. When ANOVA revealed significant treatment differences by the impact of salinity, temperature, and their interaction (salinity × temperature), Duncan's multiple tests (p = 0.05, p = 0.01) were carried out to perform all-pairwise comparison between the treatment means [55].

3. Results

3.1. Effect of Temperature and Salinity on Germination Indices

Temperature (A), salinity (B), and their combination (A \times B) significantly (*p* = 0.0001) affected the germination percentage (GP) of L. scindicus seeds (Supplementary Table S1). The GP was the highest in non-saline-treated seeds at both the temperatures (i.e., T1 = 25/20 °C and T2 = $35/30 \circ C$, D/N) applied, followed by the GP of seeds sown at 50 mM salinity stress (Figure 1A). At the highest levels of salinity (i.e., 100 and 150 mM), the seeds incubated at T2 showed a significant decline in the GP. The same pattern was found in germination speed, where the non-saline-treated seeds and those with 50 mM salinity stress germinated faster at both the temperatures T1 and T2 (Figure 2A,B). The non-saline seeds at T2 reached the maximum germination on the 6th day, while, as in T1, the peak germination of non-salinetreated seeds was achieved on the 8th day. For the highest salinity levels, the germination was inhibited for the first few days. However, the germination of *L. scindicus* was completely inhibited at 200 mM NaCl at both temperature levels. The temperature had no significant effect on the GR of the L. scindicus seeds, but it showed an abrupt decline with the increasing salinity (p < 0001, Figure 1B). The highest GR was recorded in non-saline-treated seeds incubated at T2 (3.5 seeds/day), followed by seeds treated with 50 mM NaCl stress at T1. Additionally, the seed vigor index (SVI) constantly showed a decline with increasing salinity levels (Figure 1C). The results also revealed a significant effect of temperature on the SVI, with the seeds germinated at T2 showing a consistent decrease at all NaCl concentrations. The highest decline was observed in 150 mM-salinity-treated seeds.

Recovery germination of the *L. scindicus* seeds increased with the increasing NaCl concentrations after transferring them to distilled water (Figure 3, Supplementary Table S2). Aside from the fact that the seeds treated with the higher salinities, such as 200 mM NaCl, did not germinate, large proportions of these seeds recovered after being transferred to distilled water. The highest recovery percentage was recorded in the seeds with the highest level of salinity stress (200 mM) at the optimum temperature T1 (85%), followed by the seeds treated with 150 mM NaCl stress at both T2 (83.5%) and T1 (82.2%).



Figure 1. Effect of temperature and salinity on the germination parameters of *L. scindicus* seeds. (A) germination percentage; (B) germination rate; and (C) seed vigor index. Bars represent the mean values and nails on the top indicate standard error. Capital and small letters indexed on the top of the bars represent the significance of the temperature and salinity effect, respectively, at p = 0.05, Duncan's test.



Figure 2. Cumulative germination speed of *L. scindicus* seeds at different temperatures and salinity levels. (A) temperature 1 and (B) temperature 2. Each bar is a representation of the mean (n = 5) values and the nails on the top indicate standard error.



Figure 3. Effect of temperature and salinity on recovery germination of *L. scindicus* seeds. Bars represent the mean values and nails on the top indicate standard error. Capital and small letters indexed on the top of the bars represent the significance of the temperature and salinity effect, respectively, at p = 0.05, Duncan's test.

3.2. Seedling Growth

The aRL and aSL decreased significantly with the increasing salt concentrations (p = 0.0001, Supplementary Table S1 and Figure S2). The highest aRL and aSL were shown in the seedlings germinated with the non-saline treatment and the lowest were recorded at the highest (150 mM) salinity level (Figure 4A,B). The temperature showed a significant effect on the aRL at all salinity levels. The maximum aRL was shown by the seedlings germinated at T1 (Figure 4A). However, in the case of the aSL, the temperature showed no significance in the seedlings germinated under non-saline conditions, while the aSL of the seedlings germinated at T1 was significantly higher compared to seedlings at T2 with all the salinity levels (50–150 mM NaCl, Figure 4B).



Figure 4. Effect of temperature and salinity on the seedling growth parameters of *L. scindicus*. (A) average root length; (B) average shoot length; (C) root dry weight; (D) shoot dry weight; (E) seedling biomass; and (F) specific leaf area. Bars represent the mean values (n = 5) and nails on the top indicate standard error. Capital and small letters indexed on the top of the bars represent the significance of the temperature and salinity effect, respectively, at p = 0.05, Duncan's test.

The RDW and SDW of the *L. scindicus* seedlings showed a significant decline with the increasing salinity (p = 0.0001, Figure 4C,D). A similar pattern was observed in the SB, as far as salinity is concerned (Figure 4E). The temperature showed no significant effect on the RDW and SDW at all the NaCl concentrations. The highest RDW was calculated in the non-saline-treated seedlings germinated at T2, while the highest SDW was shown by the 50 mM-salinity-treated seedlings germinated at T1. The most reduction in both the RDW and SDW was determined in the T2-incubated seedlings at the 150 mM salinity level. The SB showed significant variation with the change in temperature (p = 0.0001). The SB of the seedlings germinated at T1 was higher at all the salinity levels except at 150 mM NaCl, where the SB of the seedlings incubated at T1 was higher (Figure 4E).

Salinity, temperature, and their combination showed a significant effect on the specific leaf area (SLA) of the *L. scindicus* seeds (Supplementary Table S1). The SLA showed a considerable decline with increasing NaCl concentrations, except for the seedlings incubated at T1 and treated with 50 mM salinity, which showed an abrupt increase (Figure 4F). The highest SLA was determined in the seedlings grown in T1 incubators at 50 mM salinity, while the lowest was estimated in the seedlings at T2, treated with 150 mM NaCl stress.

3.3. Effect of Salinity and Temperature on Chlorophyll Content of L. scindicus Seedlings

The effects of temperature (A) and salinity (B), and their combination (A × B), on the chlorophyll content of *L. scindicus* seedlings were found to be highly significant (p < 0.0001, Supplementary Table S1). The results indicated that the salinity significantly decreased the chlorophyll *a* (Figure 5A), chlorophyll *b* (Figure 5B), and total chlorophyll (Figure 5C) content of the *L. scindicus* seedlings incubated at both T1 and T2. The optimum temperature, i.e., T1, displayed better chlorophyll pigment concentrations at all the studied salinity levels. The highest chlorophyll content accumulation was measured in non-saline-treated seedlings at T1 and the largest decline was recorded in 150 mM NaCl-treated-seedlings at T1. It is worthwhile to mention that there was not the required seedling material available for the study of the chlorophyll content at T2 at the 150 mM salinity level.

3.4. Effect of Salinity and Temperature on the Shoot and Root Proline Content of *L. scindicus Seedlings*

Increasing levels of NaCl application (0–100 mM) significantly enhanced the production of proline in the shoots and roots of the *L. scindicus* seedlings at both the applied temperatures T1 and T2 (Supplementary Table S1, Figure 6). The proline content of the shoot and root systems was higher in the seedlings germinated at T2 at all the studied salinity concentrations. The maximum proline buildup was recorded at the highest salinity stress for the seedlings germinated at T2. It is pertinent to mention that there was not enough material to investigate the proline content at the salinity level of 150 mM.



Figure 5. Effect of temperature and salinity on the chlorophyll *a* (**A**); chlorophyll *b* (**B**); and total chlorophyll (**C**) of *L. scindicus* seedlings. Bars represent the mean values (n = 5) and nails on the top indicate standard error. Capital and small letters indexed on the top of the bars represent the significance of the temperature and salinity effect, respectively, at p = 0.05, Duncan's test.



Figure 6. Effect of temperature and salinity on the shoot proline (μ g/gFW) and root proline (μ g/gFW) content of *L. scindicus* seedlings. Bars represent the mean values (*n* = 5) and nails on the top indicate standard error. Capital and small letters indexed on the top of the bars represent the significance of the temperature and salinity effect, respectively, at *p* = 0.05, Duncan's test.

4. Discussion

This study aimed to explore the effects of different salt concentrations on seed germination, seedling growth, chlorophyll content, and proline content in L. scindicus seedlings germinated at two different temperature levels. Salinity and temperature are important factors affecting seed germination [3,4]. The temperature has been shown to modulate salinity tolerance during the germination stage, with the highest tolerance found around the optimal temperature [36]. In glycophytes and to a lesser extent in halophytes, increased salt stress has been demonstrated to cause a reduction in the percentage of seed germination as well as a delay in the germination process [51,56-58]. Moreover, the ability of seeds to germinate through a wide range of salinities and temperatures is critical for the production of plants in varying environments [59]. Our findings revealed that increasing salt concentrations significantly decreased the GP, GR, and SVI at both the incubating temperature levels T1 and T2 (Figure 1). The results also indicated that the germination speed at the highest salinity levels was delayed (Figure 2). These results were in agreement with previous studies on acacia species [60], Acacia ehrenbergiana and Acacia seyal [61], Festuca arundinacea [58], Haloxylon ammodendron [62], Festuca arundinacea, Bromus inermis, and *Elymus breviaristatus* [40], and *Lasiurus scindicus* and *Panicum turgidum* [42].

Additionally, the results indicated that the seeds of *L. scindicus* incubated at 35/30 °C, D/N temperature (T2) showed a decline in germination indices such as the GP, GR, and SVI compared to the seeds germinated at T1 (optimal temperature for the germination of *L. scindicus*). However, the germination rate and/or the cumulative germination speed were higher in the case of seeds incubated at T2 under the non-saline or lower salinity concentration, which then showed a decline under the highest salinity levels. Similar results were reported by [41,42,59], where the germination of *Medicago ruthenica; Lasiurus scindicus, Panicum turgidum;* and *Sorghum bicolor* decreased at the highest temperature under the varying concentrations of NaCl. These results can be linked to the capacity of high temperatures to impede seed germination by inducing the production of large levels of endogenous abscisic acid (ABA) via transcriptional activation of ABA signaling genes [63,64]. Apparently, under higher temperatures, salinity can affect germination by directly altering seed water imbibition due to the reduced osmotic potential of germination media, and the

biochemical reactions that regulate the metabolism involved in seed germination [65,66]. Also, the effects of NaCl are increased on the osmotic potential and specific ion toxicity (accumulation of an excess of Na⁺ and Cl⁻ ions) under increasing temperatures [33,40,51]. Aside from that, the absorption of excess Na⁺ and Cl⁻ ions from soils cause ionic stress and toxicity, which contributes to the disruption in biochemical processes such as nucleic and protein metabolism, energy production, and respiration [51,67]. Salinity also disrupts nutrient and hormone balances during germination, particularly gibberellin (GA) and abscisic acid (ABA). As a result, high salinity levels cause seed germination to be delayed or even inhibited, depending on the salt tolerance of the plants [68]. High salinity stress may disrupt the dynamic balance between the generation and scavenging of reactive oxygen species (ROS) such as hydroxyl radicals (OH⁺), superoxide (O2^{•-}), and hydrogen peroxide (H₂O₂). ROS damage macromolecules such as proteins, carbohydrates, nucleic acids, and lipids, as well as cellular structures such as membranes, resulting in seed germination inhibition [69].

According to the results of the recovery germination, ungerminated *L. scindicus* seeds from the two incubating temperatures and exposed to high NaCl concentrations for 20 days germinated successfully after being transferred to distilled water (Figure 3). The results in this study were in accordance with [70,71], where the results also indicated the recovery of ungerminated *Arthrocnemum macrostachyum*, *Arthrocnemum indicum*, and *Atriplex canescens* seeds from high salinity levels. Recovery of germination indicates the ability of seeds to survive in harsh environments. Seed survival rather than germination is the more effective method for plants to establish successfully under elevated salt stress conditions, because germination occurs when high-saline conditions are alleviated, such as during a rainy season [70].

In addition to seed germination, increased salt and temperature had detrimental effects on seedling growth, as measured by the root length, shoot length, and seedling biomass. The seedling growth parameters such as the aRL, aSL, RDW, SDW, SB, and SLA of *L. scindicus* showed a significant decline with the increasing salinities at both the incubating temperatures of T1 and T2 (Figure 4). This is a common phenomenon in plants under salinity stress [72]. Many plants experience a reduction in seedling root and shoot lengths under saline conditions. This could be due to the harmful effects of NaCl, as well as a lack of water and nutrient intake [73]. Furthermore, salt can have a deleterious impact on cells, tissue, and organ ultrastructure [8]. Secondly, salinity, through osmotic and specific ion toxic effects, prevents the preservation of sufficient nutrient levels important for plant growth, reducing root and shoot emergence, and seedling growth [20,21,74]. Our findings are in line with the results of [51,58], where the seedling growth of Sorghum bicolor and *Festuca arundinacea* showed a constant decline with the increase in salinity treatment. Moreover, the exposure of plants to high temperatures can have morphological implications, such as sunburn on the entire plant's shoot, leaf senescence, and root and shoot growth inhibition [75]. The results of our study indicated that the aRL, aSL, and SLA of *L. scindicus* seedlings decreased when incubated at T2 along with all the varying salinity concentrations. These results are in accordance with the findings of [59], where all the growth parameters of Sorghum bicolor showed a significant decline at the highest temperature of 40 °C. This is due to the increased detrimental impact of high temperatures on enzymic activities, protein synthesis, and ATP content, as well as the generation of reactive oxygen species (ROS) [27].

Plants' responses to excessive salinity have been shown to have a negative impact on photosynthetic activity, resulting in a decrease in chlorophyll concentration [76]. This decrease in chlorophyll concentration could be attributed to the loss of grana stacking or to changes in the thylakoid structure [77]. The results indicated a general declining trend of chlorophyll *a*, chlorophyll *b*, and total chlorophyll in *L. scindicus* seedlings when exposed to increasing salinity concentrations at two incubating temperatures T1 and T2 (Figure 5). Also, the chlorophyll content of the seedlings showed an abrupt decline at the temperature T2 compared to the seedlings at T1 with all the salinity levels. These results indicate that the response to high salinity and temperature involves a drop in the chlorophyll content of *L. scindicus* plants, as also shown in the previous studies on *L. scindius* [8], *Sorghum bicolor* [59], and *P. simonii* [78].

Proline, a suitable osmolyte, is accumulated in plants in response to abiotic stress such as salinity, and low and high temperature [79]. This molecule has a variety of protective functions, including cellular structure stabilization and damage reduction in the photosynthetic apparatus, redox status balance, cytosolic pH maintenance, protein structure stabilization, and participation in stress signaling [80]. It also acts as an antioxidant and an ROS scavenger [81]. Moreover, proline metabolism plays an important role in seed germination via the oxidative pentose phosphate pathway (OPPP), which relies on proline metabolism to generate NAD(P)+ in the cytosol [82]. The proline content (for both the root and shoot) in this study showed a significant increase with the increase in salinity stress and temperature (Figure 6). Similar results were observed in *Brassica napus* and tobacco plants, wherein salinity and temperature induced the accumulation of proline [83,84]. Proline overproduction has been linked to halophytic behavior in several plant species with the goal of providing salinity tolerance [81]. Furthermore, it has recently been discovered that proline helps to alleviate the effects of heat stress [84].

5. Conclusions

In conclusion, this study was carried out to evaluate the germination and stability of L. scindicus seeds incubated at two temperature levels and exposed to varying salinity stress. The results in this study demonstrated that, under a low level of salinity stress, L. scindicus seeds, incubated at two varying temperatures, can germinate and grow successfully, while with the increasing salinity concentration, there is a consistent decline both in germination and growth. The same was true for the incubation temperatures, as the L. scindicus seeds at the highest temperature, T2, showed a progressive decline compared to at T1. For example, at optimum incubation temperature T1, the seed germination under salinity level 100 mM was significantly higher (82%) than at the highest incubation temperature T2 (21%). However, the ungerminated seeds did not lose their viability on exposure to high salinity stress as they restored germination after being transferred to distilled water. The growth and physiological parameters showed a similar trend and indicated that L. scindicus was more resistant to salinity stress, especially when incubated under the optimum temperature. Seed germination research is critical for establishing a scientific and theoretical foundation for large-scale *L. scindicus* ecosystem restoration, enhancement, and protection under changing environments. This can also help with sustainable development in dry and saline areas, as well as vegetation restoration and ecosystem reconstruction, which is otherwise degrading at an enormous pace with the increase in global warming and salinity.

However, this experiment has been conducted in completely controlled conditions. The results in natural conditions may vary owing to various environmental factors. Therefore, conducting germination trial experiments in natural habitats would provide us with a better understanding.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/su14148387/s1, Table S1: Analysis of variance for different germination and growth parameters of *L. scindicus* under increasing salinity and temperature levels; Table S2: Analysis of variance for recovery germination of *L. scindicus* seeds under different salinity levels and temperature; Figure S1: Monthly temperature data of Riyadh region, Saudi Arabia; Figure S2: Showing seedlings of *L. scindicus* germinated at two temperatures T1 (A) and T2 (B), and exposed to different salinity levels.

Author Contributions: Conceptualization, J.A.M. and B.A.D.; methodology, J.A.M., B.A.D. and M.M.H.; software, B.A.D. and J.A.M.; formal analysis, J.A.M. and B.A.D.; investigation, J.A.M. and M.M.H.; resources, A.A.A., M.N.A. and J.A.M.; data curation, J.A.M., M.M.H. and B.A.D.; writing—original draft preparation, J.A.M.; writing—review and editing, M.N.A., A.A.A., B.A.D., M.M.H., S.N.S.I. and J.A.M.; visualization, J.A.M. and B.A.D.; supervision, A.A.A.; project administration, A.A.A. and M.N.A. All authors have read and agreed to the published version of the manuscript.

Funding: The authors extend their appreciation to Princess Nourah bint Abdulrahman University Researchers Supporting Project number (Grant No. PNURSP2022R103), Princess Nourah bint Abdulrahman University, Riyadh, Saudi Arabia.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

References

- 1. Poudel, R.; Finnie, S.; Rose, D.J. Effects of wheat kernel germination time and drying temperature on compositional and end-use properties of the resulting whole wheat flour. *J. Cereal Sci.* **2019**, *86*, 33–40. [CrossRef]
- 2. Nimbalkar, M.S.; Pawar, N.V.; Pai, S.R.; Dixit, G.B. Synchronized variations in levels of essential amino acids during germination in grain Amaranth. *Braz. J. Bot.* 2020, 43, 481–491. [CrossRef]
- Weber, D. Adaptive mechanisms of halophytes in desert regions. In Salinity and Water Stress; Springer: Berlin/Heidelberg, Germany, 2009; pp. 179–185.
- Farooq, S.; Onen, H.; Tad, S.; Ozaslan, C.; Mahmoud, S.F.; Brestic, M.; Zivcak, M.; Skalicky, M.; El-Shehawi, A.M. The influence of environmental factors on seed germination of *Polygonum perfoliatum* L.: Implications for management. *Agronomy* 2021, *11*, 1123. [CrossRef]
- 5. Fenner, M. Seeds: The Ecology of Regeneration in Plant Communities; CAB International: Wallingford, UK, 2000.
- Gairola, S.; Shabana, H.A.; Al Ketbi, A.; Mahmoud, T. Seed germination behavior of halophytes distributed in arid arabian deserts: A review of current research. In *Handbook of Halophytes: From Molecules to Ecosystems towards Biosaline Agriculture*; Springer: Berlin/Heidelberg, Germany, 2020; pp. 1–17.
- Etesami, H.; Noori, F. Soil salinity as a challenge for sustainable agriculture and bacterial-mediated alleviation of salinity stress in crop plants. In Saline Soil-Based Agriculture by Halotolerant Microorganisms; Springer: Berlin/Heidelberg, Germany, 2019; pp. 1–22.
- Malik, J.A.; AlQarawi, A.A.; Dar, B.A.; Hashem, A.; Alshahrani, T.S.; AlZain, M.N.; Habib, M.M.; Javed, M.M.; Abd-Allah, E.F. Arbuscular mycorrhizal fungi isolated from highly saline "sabkha habitat" soil alleviated the NaCl-induced stress and improved *Lasiurus scindicus* Henr. growth. *Agriculture* 2022, *12*, 337. [CrossRef]
- Zhang, T.T.; Qi, J.G.; Gao, Y.; Ouyang, Z.T.; Zeng, S.L.; Zhao, B. Detecting soil salinity with MODIS time series VI data. *Ecol. Indic.* 2015, 52, 480–489. [CrossRef]
- 10. Wang, F.; Xu, Y.G.; Wang, S.; Shi, W.; Liu, R.; Feng, G.; Song, J. Salinity affects production and salt tolerance of dimorphic seeds of *Suaeda salsa*. *Plant Physiol. Biochem.* **2015**, *95*, 41–48. [CrossRef]
- 11. Qu, X.X.; Huang, Z.Y.; Baskin, J.M.; Baskin, C.C. Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub *Halocnemum strobilaceum*. *Ann. Bot.* **2008**, *101*, 293–299. [CrossRef]
- 12. El-Keblawy, A.; Gairola, S.; Bhatt, A. Maternal salinity environment affects salt tolerance during germination in *Anabasis setifera*: A facultative desert halophyte. *J. Arid. Land* **2016**, *8*, 254–263. [CrossRef]
- Shrivastava, P.; Kumar, R. Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi J. Biol. Sci.* 2015, 22, 123–131. [CrossRef]
- 14. Ivushkin, K.; Bartholomeus, H.; Bregt, A.K.; Pulatov, A.; Kempen, B.; De Sousa, L. Global mapping of soil salinity change. *Remote Sens. Environ.* **2019**, 231, 111260. [CrossRef]
- 15. Dai, X.; Huo, Z.; Wang, H. Simulation for response of crop yield to soil moisture and salinity with artificial neural network. *Field Crops Res.* **2011**, *121*, 441–449. [CrossRef]
- Din, B.U.; Sarfraz, S.; Xia, Y.; Kamran, M.A.; Javed, M.T.; Sultan, T.; Munis, M.F.H.; Chaudhary, H.J. Mechanistic elucidation of germination potential and growth of wheat inoculated with exopolysaccharide and ACC-deaminase producing *Bacillus strains* under induced salinity stress. *Ecotoxicol. Environ. Saf.* 2019, 183, 109466.
- 17. Munns, R.; Tester, M. Mechanisms of salinity tolerance. Annu. Rev. Plant Biol. 2008, 59, 651–681. [CrossRef]
- 18. Fayaz, F.; Zahedi, M. Beneficial effects of arbuscular mycorrhizal fungi on wheat (*Triticum aestivum* L.) nutritional status and tolerance indices under soil salinity stress. *J. Plant Nutr.* **2021**, *45*, 185–201. [CrossRef]
- 19. Sofy, M.; Mohamed, H.; Dawood, M.; Abu-Elsaoud, A.; Soliman, M. Integrated usage of *Trichoderma harzianum* and biochar to ameliorate salt stress on spinach plants. *Arch. Agron. Soil Sci.* 2021, 1–22. [CrossRef]
- 20. Kumar, S.; Li, G.; Yang, J.; Huang, X.; Ji, Q.; Liu, Z.; Ke, W.; Hou, H. Effect of salt stress on growth, physiological parameters, and ionic concentration of water dropwort (*Oenanthe javanica*) cultivars. *Front. Plant Sci.* **2021**, *12*, 660409. [CrossRef]
- Tang, X.; Mu, X.; Shao, H.; Wang, H.; Brestic, M. Global plant-responding mechanisms to salt stress: Physiological and molecular levels and implications in biotechnology. *Crit. Rev. Biotechnol.* 2015, 35, 425–437. [CrossRef]
- Liu, L.; Huang, L.; Lin, X.; Sun, C. Hydrogen peroxide alleviates salinity-induced damage through enhancing proline accumulation in wheat seedlings. *Plant Cell Rep.* 2020, 39, 567–575. [CrossRef]

- 23. Baskin, C.C.; Baskin, J.M. Seeds: Ecology, Biogeography, and, Evolution of Dormancy and Germination; Elsevier: Amsterdam, The Netherlands, 1998.
- Prerna, D.I.; Govindaraju, K.; Tamilselvan, S.; Kannan, M.; Vasantharaja, R.; Chaturvedi, S.; Shkolnik, D. Influence of nanoscale micro-nutrient α-Fe₂O₃ on seed germination, seedling growth, translocation, physiological effects and yield of rice (*Oryza sativa*) and maize (*Zea mays*). *Plant Physiol. Biochem.* 2021, *162*, 564–580. [CrossRef]
- 25. Koger, C.H.; Reddy, K.N.; Poston, D.H. Factors affecting seed germination, seedling emergence, and survival of texasweed (*Caperonia palustris*). *Weed Sci.* 2004, *52*, 989–995. [CrossRef]
- Bidgoly, R.O.; Balouchi, H.; Soltani, E.; Moradi, A. Effect of temperature and water potential on *Carthamus tinctorius* L. seed germination: Quantification of the cardinal temperatures and modeling using hydrothermal time. *Ind. Crops Prod.* 2018, 113, 121–127. [CrossRef]
- Khaeim, H.; Kende, Z.; Jolánkai, M.; Kovács, G.P.; Gyuricza, C.; Tarnawa, Á. Impact of temperature and water on seed germination and seedling growth of maize (*Zea mays* L.). *Agronomy* 2022, 12, 397. [CrossRef]
- Blackport, R.; Screen, J.A. Insignificant effect of Arctic amplification on the amplitude of midlatitude atmospheric waves. *Sci. Adv.* 2020, *6*, eaay2880. [CrossRef]
- Khan, M.A.; Qaiser, M. Halophytes of Pakistan: Characteristics, distribution and potential economic usages. In Sabkha Ecosystems; Springer: Berlin/Heidelberg, Germany, 2006; pp. 129–153.
- 30. Bai, H.; Xiao, D.; Wang, B.; Liu, D.L.; Feng, P.; Tang, J. Multi-model ensemble of CMIP6 projections for future extreme climate stress on wheat in the North China Plain. *Int. J. Climatol.* **2021**, *41*, E171–E186. [CrossRef]
- Walck, J.L.; Hidayati, S.N.; Dixon, K.W.; Thompson, K.; Poschlod, P. Climate change and plant regeneration from seed. *Glob. Change Biol.* 2011, 17, 2145–2161. [CrossRef]
- 32. Mondoni, A.; Rossi, G.; Orsenigo, S.; Probert, R.J. Climate warming could shift the timing of seed germination in alpine plants. *Ann. Bot.* **2012**, *110*, 155–164. [CrossRef]
- Utset, A.; Borroto, M. A modeling-GIS approach for assessing irrigation effects on soil salinisation under global warming conditions. *Agric. Water Manag.* 2001, 50, 53–63. [CrossRef]
- Wang, H.; Wu, Z.; Chen, Y.; Yang, C.; Shi, D. Effects of salt and alkali stresses on growth and ion balance in rice (*Oryza sativa* L.). *Plant Soil Environ.* 2011, 57, 286–294. [CrossRef]
- 35. Ashraf, M.; Harris, P.J. Photosynthesis under stressful environments: An overview. Photosynthetica 2013, 51, 163–190. [CrossRef]
- El-Keblawy, A.; Al-Ansari, F.; Hassan, N.; Al-Shamsi, N. Salinity, temperature and light affect germination of Salsola imbricata. Seed Sci. Technol. 2007, 35, 272–281. [CrossRef]
- 37. Gorai, M.; Neffati, M. Germination responses of *Reaumuria vermiculata* to salinity and temperature. *Ann. Appl. Biol.* **2007**, 151, 53–59. [CrossRef]
- Khan, M.A.; Gulzar, S. Light, salinity, and temperature effects on the seed germination of perennial grasses. Am. J. Bot. 2003, 90, 131–134. [CrossRef] [PubMed]
- 39. Song, J.; Shi, W.; Liu, R.; Xu, Y.; Sui, N.; Zhou, J.; Feng, G. The role of the seed coat in adaptation of dimorphic seeds of the euhalophyte *Suaeda salsa* to salinity. *Plant Species Biol.* **2017**, *32*, 107–114. [CrossRef]
- 40. Liu, Y.; Zhang, S.; De Boeck, H.J.; Hou, F. Effects of temperature and salinity on seed germination of three common grass species. *Front. Plant Sci.* **2021**, *12*, 731433. [CrossRef]
- 41. Guan, B.; Zhou, D.; Zhang, H.; Tian, Y.; Japhet, W.; Wang, P. Germination responses of *Medicago ruthenica* seeds to salinity, alkalinity, and temperature. *J. Arid. Environ.* **2009**, *73*, 135–138. [CrossRef]
- 42. El-Keblawy, A.; Al-Ansari, F.; Al-Shamsi, N. Effects of temperature and light on salinity tolerance during germination in two desert glycophytic grasses, *Lasiurus scindicus* and *Panicum turgidum*. *Grass Forage Sci.* 2011, 66, 173–182. [CrossRef]
- Sanadya, S.K.; Shekhawat, S.S.; Sahoo, S. Sewan grass: A potential forage grass in arid environments. In Grasses and Grassland-New Perspectives; IntechOpen Limited: London, UK, 2021.
- 44. Assaeed, A.M.; Al-Doss, A.A. Seedling competition of *Lasiurus scindicus* and *Rhazya stricta* in response to water stress. *J. Arid. Environ.* **2001**, *49*, 315–320. [CrossRef]
- Chaudhary, S.A.; Al-Jowaid, A.A.A. Vegetation of the Kingdom of Saudi Arabia; National Agricultural and Water Research Center, Ministry of Agriculture and Water: Riyadh, Saudi Arabia, 1999.
- Cunningham, P.L. Plants included in the diet of Arabian sand gazelle (*Reem*) from Saudi Arabia. J. King Saud Univ.-Sci. 2013, 25, 167–173. [CrossRef]
- Qureshi, A.S. Sustainable use of marginal lands to improve food security in the United Arab Emirates. J. Exp. Biol. Agric. Sci. 2017, 5, S41–S49. [CrossRef]
- 48. Chauhan, S.S. Desertification control and management of land degradation in the Thar desert of India. *Environmentalist* **2003**, *23*, 219–227. [CrossRef]
- Naz, N.; Rafique, T.; Hameed, M.; Ashraf, M.; Batool, R.; Fatima, S. Morpho-anatomical and physiological attributes for salt tolerance in sewan grass (*Lasiurus scindicus* Henr.) from Cholistan Desert, Pakistan. *Acta Physiol. Plant.* 2014, 36, 2959–2974. [CrossRef]
- 50. El-Sheikh, M.A.; Thomas, J.; Alatar, A.A.; Hegazy, A.K.; Abbady, G.A.; Alfarhan, A.H.; Okla, M.I. Vegetation of Thumamah Nature Park: A managed arid land site in Saudi Arabia. *Rend. Lincei* **2013**, *24*, 349–367. [CrossRef]

- 51. Rajabi Dehnavi, A.; Zahedi, M.; Ludwiczak, A.; Cardenas Perez, S.; Piernik, A. Effect of salinity on seed germination and seedling development of sorghum *bicolor* (L.) Moench) genotypes. *Agronomy* **2020**, *10*, 859. [CrossRef]
- 52. Bajji, M.; Kinet, J.-M.; Lutts, S. Osmotic and ionic effects of NaCl on germination, early seedling growth, and ion content of *Atriplex halimus (Chenopodiaceae). Can. J. Bot.* 2002, *80*, 297–304. [CrossRef]
- 53. Arnon, D.I. Copper enzymes in isolated chloroplasts. Polyphenoloxidase in Beta vulgaris. Plant Physiol. 1949, 24, 1–15. [CrossRef]
- 54. Bates, L.S.; Waldren, R.P.; Teare, I. Rapid determination of free proline for water-stress studies. *Plant Soil* **1973**, *39*, 205–207. [CrossRef]
- 55. Steel, R.G.; Torrie, J.H. *Principles and Procedures of Statistics: A Biometrical Approach*; McGraw-Hill: New York, NY, USA, 1980; Volume 2, pp. 137–139.
- 56. Almodares, A.; Hadi, M.; Dosti, B. Effects of salt stress on germination percentage and seedling growth in sweet sorghum cultivars. *J. Biol. Sci.* 2007, *7*, 1492–1495. [CrossRef]
- 57. El-Keblawy, A. Salinity effects on seed germination of the common desert range grass, *Panicum turgidum. Seed Sci. Technol.* 2004, 32, 873–878. [CrossRef]
- 58. Shiade, S.R.G.; Boelt, B. Seed germination and seedling growth parameters in nine tall fescue varieties under salinity stress. *Acta Agric. Scand. Sect. B—Soil Plant Sci.* 2020, 70, 485–494. [CrossRef]
- AL-Shoaibi, A.A. Combined effects of salinity and temperature on germination, growth and gas exchange in two cultivars of Sorghum bicolor. J. Taibah Univ. Sci. 2020, 14, 812–822. [CrossRef]
- Cherifi, K.; Boufous, E.H.; Boubaker, H.; Msanda, F. Comparative Salt Tolerance Study of Some Acacia Species at Seed Germination Stage. arXiv 2016, arXiv:1610.06033.
- Ben Zetta, H.; Amrani, S.; Nacer, A.J.A.E.; Research, E. Effects of pre-germination treatments, salt and water stresses on germination of *Acacia ehrenbergiana* Hayne and *Acacia seyal* Del.(Mimosoideae): Two Algerian native species. *Appl. Ecol. Environ. Res.* 2017, 15, 355–368. [CrossRef]
- 62. Zhumabekova, Z.; Xu, X.; Wang, Y.; Song, C.; Kurmangozhinov, A.; Sarsekova, D. Effects of sodium chloride and sodium sulfate on *Haloxylon ammodendron* seed germination. *Sustainability* **2020**, *12*, 4927. [CrossRef]
- Chiu, R.S.; Nahal, H.; Provart, N.J.; Gazzarrini, S. The role of the Arabidopsis FUSCA3 transcription factor during inhibition of seed germination at high temperature. BMC Plant Biol. 2012, 12, 15. [CrossRef]
- 64. Toh, S.; Imamura, A.; Watanabe, A.; Nakabayashi, K.; Okamoto, M.; Jikumaru, Y.; Hanada, A.; Aso, Y.; Ishiyama, K.; Tamura, N.; et al. High Temperature-Induced Abscisic Acid Biosynthesis and Its Role in the Inhibition of Gibberellin Action in Arabidopsis Seeds. *Plant Physiol.* **2008**, *146*, 1368–1385. [CrossRef]
- 65. Kazemi, K.; Eskandari, H. Effects of salt stress on germination and early seedling growth of rice (*Oryza sativa*) cultivars in Iran. *Afr. J. Biotechnol.* **2011**, *10*, 17789–17792. [CrossRef]
- 66. Guo, C.; Shen, Y.; Shi, F. Effect of temperature, light, and storage time on the seed germination of *Pinus bungeana* Zucc. ex Endl.: The role of seed-covering layers and abscisic acid changes. *Forests* **2020**, *11*, 300. [CrossRef]
- 67. Mwando, E.; Han, Y.; Angessa, T.T.; Zhou, G.; Hill, C.B.; Zhang, X.Q.; Li, C. Genome-wide association study of salinity tolerance during germination in barley (*Hordeum vulgare* L.). *Front. Plant Sci.* **2020**, *11*, 118. [CrossRef] [PubMed]
- 68. Uçarlı, C. Effects of salinity on seed germination and early seedling stage. In *Abiotic Stress in Plants*; IntechOpen: London, UK, 2020; p. 211.
- 69. Ibrahim, E.A. Seed priming to alleviate salinity stress in germinating seeds. J. Plant Physiol. 2016, 192, 38–46. [CrossRef] [PubMed]
- 70. Nisar, F.; Gul, B.; Khan, M.A.; Hameed, A. Germination and recovery responses of heteromorphic seeds of two co-occurring *Arthrocnemum* species to salinity, temperature and light. *S. Afr. J. Bot.* **2019**, *121*, 143–151. [CrossRef]
- 71. Bhatt, A.; Santo, A. Germination and recovery of heteromorphic seeds of *Atriplex canescens* (Amaranthaceae) under increasing salinity. *Plant Ecol.* **2016**, 217, 1069–1079. [CrossRef]
- Arias, C.; Serrat, X.; Moysset, L.; Perissé, P.; Nogués, S. Morpho-physiological responses of alamo switchgrass during germination and early seedling stage under salinity or water stress conditions. *BioEnergy Res.* 2018, 11, 677–688. [CrossRef]
- Asaadi, A.M. Investigation of salinity stress on seed germination of *Trigonella foenum-graecum*. *Res. J. Biol. Sci.* 2009, *4*, 1152–1155.
 Krishnamurthy, L.; Serraj, R.; Hash, C.T.; Dakheel, A.J.; Reddy, B.V.J.E. Screening sorghum genotypes for salinity tolerant biomass
- production. *Euphytica* 2007, *156*, 15–24. [CrossRef]
 75. Nahar, K.; Hasanuzzaman, M.; Ahamed, K.U.; Hakeem, K.R.; Ozturk, M.; Fujita, M. Plant responses and tolerance to high temperature stress: Role of exogenous phytoprotectants. In *Crop Production and Global Environmental Issues*; Springer: Berlin/Heidelberg, Germany, 2015; pp. 385–435.
- 76. Borsai, O.; Hassan, M.A.; Negrușier, C.; Raigón, M.D.; Boscaiu, M.; Sestraș, R.E.; Vicente, O. Responses to salt stress in *Portulaca*: Insight into its tolerance mechanisms. *Plants* **2020**, *9*, 1660. [CrossRef]
- 77. Boutraa, T.; Akhkha, A.; Al-Shoaibi, A.K. Evaluation of growth and gas exchange rates of two local saudi wheat cultivars grown under heat stress conditions. *Pak. J. Bot.* 2015, 47, 27–34.
- Song, Y.; Chen, Q.; Ci, D.; Shao, X.; Zhang, D. Effects of high temperature on photosynthesis and related gene expression in poplar. *BMC Plant Biol.* 2014, 14, 111. [CrossRef]
- 79. Shin, H.; Oh, S.; Arora, R.; Kim, D. Proline accumulation in response to high temperature in winter-acclimated shoots of *Prunus persica*: A response associated with growth resumption or heat stress? *Can. J. Plant Sci.* **2016**, *96*, 630–638. [CrossRef]

- 80. El Moukhtari, A.; Cabassa-Hourton, C.; Farissi, M.; Savouré, A. How does proline treatment promote salt stress tolerance during crop plant development? *Front. Plant Sci.* 2020, *11*, 1127. [CrossRef]
- 81. Ghosh, U.K.; Islam, M.N.; Siddiqui, M.N.; Khan, M.A.R. Understanding the roles of osmolytes for acclimatizing plants to changing environment: A review of potential mechanism. *Plant Signal. Behav.* **2021**, *16*, 1913306. [CrossRef]
- 82. Signorelli, S. The fermentation analogy: A point of view for understanding the intriguing role of proline accumulation in stressed plants. *Front. Plant Sci.* **2016**, *7*, 1339. [CrossRef]
- Ashrafijou, M.; Noori, S.S.; Darbandi, A.I.; Saghafi, S.J.P. Effect of salinity and radiation on proline accumulation in seeds of canola (*Brassica napus* L.). *Plant Soil Environ*. 2010, 56, 312–317. [CrossRef]
- Cvikrová, M.; Gemperlová, L.; Martincová, O.; Vanková, R. Effect of drought and combined drought and heat stress on polyamine metabolism in proline-over-producing tobacco plants. *Plant Physiol. Biochem.* 2013, 73, 7–15. [CrossRef]