



Article The Impact of Water Potential and Temperature on Native Species' Capability for Seed Germination in the Loess Plateau Region, China

Guifang Hu, Xinyue He, Ning Wang *[®], Jun'e Liu and Zhengchao Zhou

School of Geography and Tourism, Shaanxi Normal University, Xi'an 710119, China; hgf200110@163.com (G.H.); hxy0406@snnu.edu.cn (X.H.); liujune5@163.com (J.L.); zhouzhengchao@126.com (Z.Z.)
* Correspondence: nwang123456@snnu.edu.cn

Abstract: Global warming is increasing the frequency and intensity of heat waves and droughts. One important phase in the life cycle of plants is seed germination. To date, the association of the temperature and water potential thresholds of germination with seed traits has not been explored in much detail. Therefore, we set up different temperature gradients (5-35 °C), water potential gradients (–1.2–0 MPa), and temperature imes water potential combinations for nine native plants in the Loess Plateau region to clarify the temperature and water combinations suitable for their germination. Meanwhile, we elucidated the temperature and water potential thresholds of the plants and their correlations with the mean seed mass and flatness index by using the thermal time and hydrotime models. According to our findings, the germination rate was positively correlated with the germination percentage and water potential, with the former rising and the latter decreasing as the temperature increased. Using the thermal time and hydrotime models, the seed germination thresholds could be predicted accurately, and the germination thresholds of the studied species varied with an increase in germination percentage. Moreover, temperature altered the impact of water potential on the germination rate. Overall, the base water potential for germination, but not the temperature threshold, was negatively correlated with mean seed mass and was lower for rounder seeds than for longer seeds. This study contributes to improving our understanding of the seed germination characteristics of typical plants and has important implications for the management and vegetation restoration of degraded grasslands.

Keywords: seed germination; temperature; water potential; thermal time model; hydrotime model; Loess Plateau

1. Introduction

Global climate change is associated with an increase in droughts and heat waves [1,2]. Global climate change may prevent, delay, or promote species regeneration from seeds, which may have an impact on the dynamics of plant populations and the composition of vegetation [3–5]. The impacts of climate change on plants have been extensively studied, but less attention has been paid to how these changes may affect plant regeneration [4,6]. However, based on seed germination, environment has a significant impact on plant recruitment [7–9]. Seed germination is an essential life history event in plants and can be affected by a variety of environmental factors and their interactions, such as temperature, water potential, salinity, pH, and depth of burial [10–13]. The two most important environmental variables for seed germination and the ensuing growth of seedlings are thought to be temperature and water potential [14,15]. Understanding how environmental influences affect the germination of seeds can help one not only to understand and predict the ecological adaptations of species, but also to develop effective restoration strategies [16–18].

One major environmental element that can control enzyme activity and either stimulate or prevent the generation of hormones that influence seed germination is tempera-



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Copyright: © 2024 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/). ture [15,19–21]. The germination responses of seed lots to temperature can be characterized through three cardinal temperatures [22,23]: a base temperature (T_b), below which the seeds do not germinate; an optimal temperature (T_o), at which the process proceeds at its fastest pace; and a ceiling temperature (T_c), above which the process is stopped [24–26]. These cardinal temperatures, T_b , T_c , and T_o , are associated with the range of ecological and geographic circumstances to which a particular species has evolved, and serve to couple the timing of germination with favorable conditions for subsequent growth and development [27,28]. In general, temperate-region seeds require lower temperatures than tropical-region seeds, and wild species have lower temperature requirements than domesticated plants [29–31]. Understanding the germination process when affected by temperature can help in assessing the germination characteristics or the establishment potential among range species, particularly in arid and semiarid regions [32], and can be used to identify the geographical areas appropriate to a species or genotype so it can germinate and establish [33].

Another crucial environmental component for seed germination is the availability of water [14,34]. In many parts of the world, increasing global climate change is predicted to lead to an increase in aridity [35,36]. In general, the seed germination percentage declines and mean germination time increases with decreasing water potential, and certain species may retain a reasonably high germination percentage even at very low water potential [37,38]. For example, large seeds can buffer seedlings from the negative effects of drought, and they have an advantage in establishing plants under low-soil-moisture conditions [39]. Furthermore, compared to species accustomed to humid settings, those acclimated to dry habitats may be less susceptible to water stress during seed germination [15,40]. Bradford (1990) [41] developed a hydrotime model to show how decreased water potential affects the progress of seed germination, which is used to assess germination rates at various water potentials in a way that is comparable to the thermal time model [14,41]. This threshold model quantifies the hydrotime constant (θ_H in MPa h⁻¹), the threshold water potential for germination or inherent level of osmotic tolerance (Ψ_b in MPa), and the uniformity of seed germination in the population (σ_{Ψ}), i.e., these biological parameters reflect seed vigor [42,43]. The hydrotime model hypothesizes that germination rates, or the inverse of time to germination, are positively proportional to the degree to which the water potential of the growing medium surpasses the base or threshold value necessary for the seeds to germinate [44,45].

The most vital phase of plant development and the beginning point of a new population is thought to be seed germination [14,19,46]. In addition, it is one of the more delicate phases of life and can easily result in seed inactivation or failure of establishment [47]. For example, seed germination is driven by environmental factors (especially climatic variables), such as temperature and humidity conditions in the seedbed, and it is related to seed traits, such as size and shape [48]. Seed germination responds differently to temperature and moisture availability in different species and/or populations [49], but few studies incorporate seed traits (e.g., size, shape, etc.) when assessing the response of germination to temperature and moisture effectiveness. The shape and size of seeds have a considerable impact on the germination process and also affect the seed hardiness, vigor, and quantity of stored carbohydrates, thus affecting the success or failure of the seedling [10,50-52]. According to theoretical research, flat, elongated seeds should germinate more frequently than round seeds [53]. Moreover, when it comes to seed germination and seedling survival, large-seeded species frequently have an advantage over small-seeded ones [54]. Seed characteristics determine the dynamics of plant communities and shed light on how different species have adapted to environmental constraints and community structure [55].

The Loess Plateau, which is located in northern China, is one of the most severely eroded areas in the world [56] and lies in a typical arid and semiarid region [57]. The ecosystem in this region is under threat of degradation due to long-term soil erosion disturbance and drought stress, and natural vegetation regeneration and restoration are effective ways to curb ecological degradation [58]. However, the hilly–gullied Loess Plateau

region is characterized by an arid climate and water deficit, which are serious constraints to vegetation restoration and ecological construction [59]. Therefore, understanding the effects of environmental factors on seed germination would be useful for conservation and restoration. The most crucial elements in seed germination and seedling establishment, according to earlier research, are temperature and water potential [60]. However, not much research has been conducted to date on the region's base water potential and temperature threshold—also referred to as the three cardinal temperatures—for seed germination [14,61]. In addition, it is unknown how base water potential, temperature threshold, and seed size and shape relate to plant germination.

Therefore, we performed a series of laboratory experiments on nine plant species from the hilly–gullied Loess Plateau region to address the following questions: (1) What impact do temperature and water potential have individually and together on native plant seed germination? (2) What is the base water potential and temperature threshold for germination in these species? (3) How do various plants respond when it comes to temperature and water stress during germination? (4) How do temperature and base water potential thresholds for germination relate to seed traits (size, shape)? (5) What are the appropriate temperature and moisture combinations for germination in these species? In general, this study contributes to a deeper understanding of the impact of changes in climatic variables (temperature, moisture) on the seed germination of plant populations in the hilly–gullied Loess Plateau region; additionally, it increases our understanding of the ecological adaptations of species and enables us to formulate effective strategies for restoration.

2. Results

2.1. Germination Responses to Temperature

The germination rate and percentage of nine native plant species from the loess hilly areas were significantly impacted by temperature. (p < 0.05, Figure 1). The germination rate and percentage of all species generally exhibited a tendency to rise, and then, fall with temperature (Figure 1). High or low temperatures inhibited the germination of different species to different degrees, and the germination percentage and rate of the studied seeds were higher at 15–30 °C than at 5–10 °C and 35 °C. For example, at 5 °C, only Artemisia sacrorum and Periploca sepium germinated, and the seeds of the other species did not germinate (Figure 1). Most species had low germination rates, except for some heat-tolerant plants such as *P. sepium* and *Linum usitatissmum* (Figure 1). The estimations of T_b , T_o , and T_c were extrapolated using the linear relationship between germination rate and temperature. In addition, germination temperature thresholds were influenced by seed germination percentage (g) and varied with germination percentage between species (Figure 2, Table S1), making it difficult to determine a universal pattern. Linear increases and reductions in the germination rates below and above the T_o were seen when the germination rates for various percentiles were plotted versus temperature. Specifically, Lespedeza davurica seeds could germinate in a variety of temperature ranges, whereas Bothriochloa ischaemum, L. usitatissmum, and Sophora davidii had a smaller range of germination temperatures and were more sensitive to temperature than the rest of the species. Figure 3 illustrates how the thermal time model may be used to estimate seed germination thresholds (Figure 3) more precisely. For most of the species under study, the goodness of fit between actual and anticipated germination rates was above 80% (Figure 3). The nine species were split into four distinct subgroups using heat maps or cluster analyses based on how the temperature affected the germination rate and germination percentage (Figure 4A). Specifically, one subgroup was *P. sepium*, which showed high tolerance for high temperatures, and another subgroup included *A. sacrorum*, which was more tolerant to cold than the rest of the species.



Figure 1. Percentage and rate $(1/T_{50})$ of seed germination in nine species at seven different temperatures. Different uppercase letters indicate that germination percentage differed significantly (p < 0.05) between temperature treatments; Different lowercase letters indicate that germination rate $(1/T_{50})$ differed significantly (p < 0.05) between temperature treatments; (**A**) *Artemisia scoparia*, (**B**) *Artemisia giraldii*, (**C**) *Artemisia sacrorum*, (**D**) *Periploca sepium*, (**E**) *Bothriochloa ischaemum*, (**F**) *Patrinia scabiosifolia*, (**G**) *Linum usitSatissimum*, (**H**) *Lespedeza davurica*, (**I**) *Sophora davidii*.



Figure 2. Linear regression of temperatures and percentages of germination $(1/t_g)$ in nine species at various percentiles where t_g is the time to reach a specific germination percentage (d); (A) *Artemisia scoparia*, (B) *Artemisia giraldii*, (C) *Artemisia sacrorum*, (D) *Periploca sepium*, (E) *Bothriochloa ischaemum*, (F) *Patrinia scabiosifolia*, (G) *Linum usitatissimum*, (H) *Lespedeza davurica*, (I) *Sophora davidii*.



Figure 3. Linear fit of observed and predicted germination rates of nine species. The blue line represents the fitted trend line of the observed germination rates to the predicted germination rates; the dots represent the predicted germination rates (predicted by the thermal time model) for various observed germination rates. (**A**) *Artemisia scoparia*, (**B**) *Artemisia giraldii*, (**C**) *Artemisia sacrorum*, (**D**) *Periploca sepium*, (**E**) *Bothriochloa ischaemum*, (**F**) *Patrinia scabiosifolia* (**G**) *Linum usitatissimum*, (**H**) *Lespedeza davurica*, (**I**) *Sophora davidii*.



Figure 4. The clustering analysis of germination percentages and rates $(1/T_{50})$ under different treatments among nine species; (**A**) germination percentages and rates $(1/T_{50})$ for temperature treatments; (**B**) germination percentages and rates $(1/T_{50})$ for water potential treatments.

2.2. Germination Responses to the Water Potential

Moisture had a significant impact on the germination percentages and rates of nine native plants of the loess hilly regions (p < 0.05, Figure 5). Germination percentages and rates decreased as water potential decreased; however, different plants responded to drought stress differently. For example, the germination percentage of *S. davidii* reached more than 80% under all five water potential treatments, while Patrinia scabiosifolia's germination percentage and germination rate were close to 0 at -1.2 MPa (Figure 5). In addition, S. davidii and L. usitatissmum had a wide range of tolerance to drought stress, with their base water potentials lower than -2 MPa, while *P. sepium* had a very sensitive tolerance to the water potentials, with a base water potential of about -1.3 MPa (Table S2). Linear regression of the germination rate and water potential of the studied species revealed that the germination rate was significantly positively correlated with the water potential (Figure S1), and that the base water potential varied weakly with the germination rate (g) (Figure S1, Table S2). As shown in Figure 6, the hydrotime model was well fitted for all species, with a goodness of fit of more than 80% between observed and predicted germination rates for the vast majority of the studied species (Figure 6). Heat map or cluster analysis divided the nine species into three different subgroups according to the response of germination percentages and rates to water potential (Figure 4B). One subgroup was P. scabiosifolia, B. ischaemum, and P. sepium, which showed weak drought tolerance, and another subgroup was A. sacrorum, Artemisia giraldii, and Artemisia scoparia, which showed high drought tolerance (Figure 4B).



Figure 5. Percentage and rate $(1/T_{50})$ of seed germination in nine species at five different water potential treatments; Different uppercase letters indicate that germination percentage differed significantly (p < 0.05) between water potential treatments; Different lowercase letters indicate that germination rate $(1/T_{50})$ differed significantly (p < 0.05) between water potential treatments; (**A**) *Artemisia scoparia*, (**B**) *Artemisia giraldii*, (**C**) *Artemisia sacrorum*, (**D**) *Periploca sepium*, (**E**) *Bothriochloa ischaemum*, (**F**) *Patrinia scabiosifolia*, (**G**) *Linum usitatissimum*, (**H**) *Lespedeza davurica*, (**I**) *Sophora davidii*.



Figure 6. Linear fit of observed and predicted germination rates of nine species. The green line represents the fitted trend line of the observed germination rates to the predicted germination rates; the dots represent the predicted germination rates (predicted by the hydrotime model) for various observed germination rates. (A) *Artemisia scoparia*, (B) *Artemisia giraldii*, (C) *Artemisia sacrorum*, (D) *Periploca sepium*, (E) *Bothriochloa ischaemum*, (F) *Patrinia scabiosifolia*, (G) *Linum usitatissimum*, (H) *Lespedeza davurica*, (I) *Sophora davidii*.

2.3. Germination Responses to the Interaction of Temperature and Water Potential

Moisture and temperature are determinants of seed germination, and these two factors can individually or jointly affect germination percentage. The results of a two-way ANOVA on the studied species showed that the interaction of Species $\times T$, Species $\times \Psi$, $T \times \Psi$, and Species $\times T \times \Psi$ had a significant impact on the germination percentage (p < 0.001). At the same temperature, the germination percentage of most species decreased with decreasing water potential, but the response of different species to water potential varied with temperature. For example, the inhibitory effect of drought stress on germination in most species was more pronounced at 30 °C than at other temperatures (Figure 7). However, at 15 °C, drought stress appeared to more significantly inhibit the germination of the heattolerant *P. sepium*, *B. ischaemum*, and *L. usitatissmum* than that of the other species (Figure 7). In addition, temperature can modify the effect of water potential on the germination percentage; under the appropriate temperature, seeds can also achieve a high germination percentage under low water potential. For example, the germination percentage of S. davidii at -1.2 MPa also exceeded 80% at 20 °C (Figure 7). At all temperature levels, all species except S. davidii had the highest germination percentage at 0 MPa (Figure 7). Meanwhile, according to the analysis of the influences of temperature-and-water potential interactions on seed germination, the optimal temperature and moisture combinations were as follows: A. scoparia: 15 °C, 0 MPa; A. giraldii: 15 °C, 0 MPa; A. sacrorum: 25 °C, 0 MPa; P. sepium:



30 °C, 0 MPa; *B. ischaemum*: 30 °C, 0 MPa; *P. scabiosifolia*: 30 °C, 0 MPa; *L. usitatissmum*: 20 °C, -0.3 MPa; *L. davurica*: 25 °C, 0 MPa; *S. davidii*: 25 °C, -0.6 MPa.

Figure 7. Interactions of temperature and water potential on the germination percentage of nine species; (A) *Artemisia scoparia*, (B) *Artemisia giraldii*, (C) *Artemisia sacrorum*, (D) *Periploca sepium*, (E) *Bothriochloa ischaemum*, (F) *Patrinia scabiosifolia*, (G) *Linum usitatissimum*, (H) *Lespedeza davurica*, (I) *Sophora davidii*.

2.4. Relationships between Germination Thresholds and Seed Traits

The temperature thresholds for seed germination varied among the nine tested species (Table S1). Among them, the base temperature was the lowest in *P. scabiosifolia* and the highest in *B. ischaemum* (Table S1). A linear fit of mean seed mass to T_b revealed a weak positive correlation (Figure 8A), whereas there was a weak negative correlation between FI and base temperature (Figure 8C). Among the tested species, the optimal germination temperature was the lowest in L. davurica and the highest in P. sepium (Table S1). Meanwhile, the optimal temperature was negatively correlated with mean seed mass and positively correlated with FL but the correlation was not significant (p > 0.05, Figure 8A,C). The ceiling temperatures were lowest in *P. scabiosifolia* and highest in *L. davurica* (Table S1). Ceiling temperature was not correlated with mean seed mass, while there was a positive correlation with FI (Figure 8). The base water potential for germination also varied among species; it was highest in *P. sepium*, lowest in *S. davidii*, and ranged from -1.33 MPa to -2.07 MPa for the other species (Table S2). A significant negative relationship existed between base water potential and mean seed mass (p < 0.05, Figure 8B), and larger seeds had lower base water potentials than smaller seeds. In addition, the relationship between FI and base water potential was positive (Figure 8D), i.e., round seeds had lower base water potentials than elongated seeds.



Figure 8. Linear fit of mean seed mass and flatness index (FI) of temperature thresholds, and water potential thresholds for nine species. (**A**) Mean seed mass and temperature thresholds; (**B**) mean seed mass and water potential thresholds; (**C**) FI and temperature thresholds; (**D**) FI and water potential thresholds.

3. Discussion

3.1. Effects of Temperature and Water Potential and Their Interaction in Seed Germination

Seed germination is an irreversible process, and once germination begins, the seedling is either self-perpetuating or dies [62]. The observation of seed radicle protrusion is a common method used to determine seed germination [63]. In many studies it is a widely accepted practice to use radicle protrusion greater than 2 mm as a criterion for determining seed germination and then calculating germination rates because this method offers a standardized and measurable indicator of seed viability and potential for successful growth. It is crucial to remember, nevertheless, that a radicle protrusion larger than 2 mm does not always imply the development of a seedling or fully grown plant [64]. For instance, poor circumstances like inadequate temperature, water, or nutrition availability may prevent a seed with a projecting radicle from developing into a viable seedling [65]. Temperature is an important factor affecting seed germination, and different plants germinate under different temperature ranges and optimal temperatures [55,66]. Temperature can speed up germination within a particular range, but extremes in temperature can hinder germination due to membrane permeability, membrane-binding activity, and the denaturation of enzymes [67,68]. The probable explanation is that suitable temperatures facilitate water uptake by the seed, enhance enzymatic processes and respiration, and store nutrients in a soluble state that is easy to use [69]. Understanding the response of plants to temperature not only helps us to understand their ecological adaptations, but also helps in developing effective vegetation restoration strategies [70]. This study's findings on the species-specific responses of seed germination to temperature are in line with other research, as various species have different optimal temperatures and temperature ranges [71]. The different responses of plants to temperature reflect their degree of adaptation to the environment, and when plants are not well adapted to the local environment they will be eliminated by the environment [72]. In addition, the temperature threshold for seed germination in

different species in the same habitat varies [15]. In this study, the thermal time model was used to derive the seed germination parameters of nine native species in the loess hilly region, and their base temperatures for germination ranged from -7.46 to $9.67 \,^{\circ}C$ (Table S1). Among them, *P. scabiosifolia* exhibited seed germination at the lowest base temperature and could even germinate under a temperature below zero, and the cluster analysis also classified *P. scabiosifolia* as a subgroup (Figure 4A). Lower base temperature (T_b) readings during germination indicate a plant's ability to withstand cold stress [73]. In addition, compared to other species, *B. ischaemum*'s germination rate and germination percentage increased more quickly as the temperature rose, and a greater base temperature was required (Figure 1), which may be because *B. ischaemum* is a C4 plant and is light and warmth loving.

These findings demonstrated that the availability of water had an impact on the percentage and rate of seed germination. Water potential has been shown to have a significant negative influence on seed germination [26]. This germination inhibition may be thought of as a seed's adaptive response to these circumstances; that is, the seeds will not germinate when exposed to lower Ψ , retaining their potential to germinate in order to reach the proper environmental conditions [29]. Distinct species have distinct hydrotime constants (θ_H) and base water potentials (Ψ_b), which affect how seeds germinate in response to water potential. The present study shows that seeds with low Ψ_b germinated better than those with high Ψ_b at a low water potential, which is consistent with Zhang et al. [34]. For example, *S. davidii* still had a germination percentage of more than 80% at -1.2 MPa, while *P. scabiosifolia* had a germination percentage close to 0 at -1.2 MPa. In addition, it is generally accepted that seeds that are suited to germinate in circumstances of water stress have an advantage when it comes to germination in arid or semiarid circumstances [74,75].

Numerous studies have found an interaction between T and Ψ regarding the percentage and rate of seed germination [76]. There was a positive correlation found between the temperature range and soil water availability of the plant in its natural environment and the capacity of seeds to germinate within that temperature range [77]. For example, tropical species often have greater T_h requirements than temperate species, whereas mesic species are less resistant to water stress (i.e., can germinate at lower water potential) than tropical plants [78–80]. The species in this study, all of which are native to the loess hilly region, have evolved traits or strategies that enable them to resist local risks, such as the ability to germinate faster in hot environments to reduce the risk of drought. Our study shows that the germination time course of the examined seeds can be accurately described by the thermal time and hydrotime models, which is in line with other research conducted at different temperatures and water potentials, respectively [76,81]. Additionally, the two models and their standard deviation offer crucial details that are vital for both biology and ecology [82]. Recent years have seen a rise in the frequency of extreme temperature swings brought on by climate change, as well as erratic precipitation and protracted droughts [83,84]. In the context of climate change, evaluating the germination characteristics and resilience of native seeds in the loess hilly region and clarifying their suitable germination conditions are significant for assessing vegetation regeneration and ecological restoration in the region.

3.2. Ecological Correlates of Seed Performance

The germination requirements for temperature and moisture vary significantly across plant populations, and seed traits can drive plant community dynamics [85]. Studying the relationship between seed morphological characteristics, environmental factors, and seed germination helps us to predict ecological population dynamics [51,86]. This study showed that small seeds have a faster germination rate than large seeds under suitable temperature conditions (Figure 1). Since small seeds are less tolerant to stressful environmental conditions, they are more sensitive to temperature changes, allowing them to germinate rapidly and in large numbers under suitable conditions [87]. However, the present study showed that there was almost no correlation between temperature threshold and seed mass, which is inconsistent with previous studies [88]. The reason for this phenomenon

may be that the temperature threshold is also influenced by other seed traits, such as seed coat thickness and permeability, which influence imbibition and germination [89,90]. Seed size showed a negative correlation with base water potential (Figure 8B), suggesting that larger seeds are more resistant to arid environments than small seeds. Seedlings raised from larger seeds are more resistant to drought, possibly because of their ability to explore larger amounts of soil to offset water scarcity, to build a more extensive root system, or to store more water [91,92]. Meanwhile, the high base water potential of small seeds is also a risk-reduction feature that results in seed germination in wetter conditions, which prevents seedlings from being exposed to dry conditions. The flatness index (FI) was positively correlated with optimal temperature, ceiling temperature, and base water potential, but none of these correlations were significant (Figure 8C,D). This may be because rounded seeds are more easily covered by soil, whereas flattened or elongated seeds are less likely to be covered by soil and are therefore more sensitive to the environment and subjected to greater stress [93].

3.3. Implications for Management and Conservation

Previous studies have demonstrated that vegetation restoration is the fundamental way to manage soil erosion in loess hilly regions [94]. However, the intra- and inter-annual temperature and precipitation variations in this region are drastic, which constrains the natural regeneration of seeds. Vegetation regeneration depends on seed germination, and there are interspecific differences in the response of germination to environmental variables [95]. Specifically, the cluster analysis showed that *P. sepium* was more tolerant to high temperatures than the other species. This may be because *P. sepium* is the species at the highest stage in the succession and can adapt to high-light habitats, so it could be considered as a species for vegetation restoration on sunny slopes in the loess hilly region. In general, large seeds are more tolerant to arid environments, so resowing large seeds rather than small seeds can be considered as a method of vegetation restoration under poor moisture conditions. Furthermore, as vegetation succession proceeds, habitat differentiation in vegetation types occurs, mainly in the upward slope direction; for example, A. giraldii is mainly distributed on sunny slopes, while A. sacrorum is mainly distributed on shady slopes [96]. Depending on the impacts of temperature and water potential on native species, it is feasible to select seasons and microhabitats (e.g., slope orientation, slope position) that are suitable for their emergence; regarding environments with harsher thermal and hydrological conditions, it is advisable to consider selecting more tolerant species for sowing to promote vegetation regeneration. Land managers should understand the seed germination needs of different populations to assure that seeds are planted at the most conducive times and under the most favorable conditions to accomplish vegetation restoration [18].

4. Materials and Methods

4.1. Study Site

The study area, Ansai, is situated in the northwest of Yan'an City, Shaanxi Province, China (109°16.7654′ E–109°17.3011′ E, 36°44.1054′ N–36°48.0715′ N), with an average altitude of 1371.9 m a.s.l. (Figure 9), and it is a typically hilly and gullied region of the Loess Plateau. The annual average temperature is about 9.8 °C, the frost-free period is about 180 days, the annual precipitation is about 660 mm, and the annual average land evaporation is about 1460 mm. The soil is mainly loess soil, with 33.2% sand, 63.2% silt, and 3.6% clay [97]. The type of vegetation belongs to the forest-steppe zone, and the dominant species are *Bothriochloa ischaemum, Stipa bungeana, Periploca sepium*, etc. The area has 58% vegetation coverage [98].



Figure 9. Map showing the location of the study site.

4.2. Seed Collection and Preparation

This study used nine native plant species with high cover from the hilly-gullied Loess Plateau region, representing the most common species used for vegetation restoration succession in the region and belonging to different families with different seed traits (size, shapes, etc.). Seeds were collected in 2019 in the small watershed of Zhifanggou and Fangta, Ansai District, Yan'an City, and stored under dry, ventilated chamber conditions for one year. The germination experiments were started in September 2020 and the sampled seeds were sterilized in 10% sodium hypochlorite solution (Shanghai, China) for 10 min and rinsed with deionized water for 5 min before the experiment. The seeds were then placed on germination medium and a viability test was carried out prior to the germination test. The germination percentage of the seeds in distilled water at room temperature was more than 80%, indicating that the seeds tested in this experiment were non-dormant [99]. We mechanically cut S. davidii and L. davurica seeds with a scalpel, stripping the seed coat to make them permeable to water. The seed mass was measured using a sensitive balance (over 1/10,000 level) (Shanghai, China) (Table 1) [100]. Meanwhile, the length (L), width (W), and height (H) of the seeds were measured using a slide caliper with four replicates, and the FI (FI = (L+W)/2 H) was used to characterize the seed shape [101]. The FI ranged from a value of 1 for spherical seeds to greater values for seeds with flat or spindle shapes [93,102].

4.3. Experimental Design

4.3.1. Temperature Effects

In this experiment, seven fixed temperatures—5, 10, 15, 20, 25, 30, and 35 °C—were utilized. A germination test was conducted with four replications by placing the seeds in Petri (Yangzhou, China) dishes measuring 90 mm in diameter on two sheets of filter paper (Hangzhou, China) saturated with 10 mL distilled water. Then, the Petri dishes were placed in a thermostatic incubator (Shanghai, China) for germination, which was programmed for a 12 h photoperiod under 0 MPa. To avoid seed germination competition due to higher density or number, we set the quantity of *P. sepium* and *L. davurica* seeds to 25 seeds; the larger seeds of *S. davidii* to 20; and the rest of the seeds to 50, according to their length, width, and height. The quantity of seeds that germinated was tallied every day, and germination was defined as when the radicle broke through the seed coat and the length of the radicle was ≥ 2 mm. A germination period of 30 days was used, and when there was no more germination after three consecutive days, the germination test was terminated.

Species	Family	Length (mm)	Width (mm)	Height (mm)	Individual Mass (g)	Shape	Appendages	FI	Seed Storage Time (Month)
Artemisia scoparia	Asteraceae	0.662 ± 0.035	0.325 ± 0.019	0.215 ± 0.013	0.020	Oval-circular	None	2.295	12
Artemisia giraldii	Asteraceae	0.923 ± 0.024	0.420 ± 0.018	0.360 ± 0.020	0.061	Oval	None	1.865	12
Artemisia sacrorum	Asteraceae	1.091 ± 0.048	0.477 ± 0.014	0.350 ± 0.030	0.085	Oval	None	2.240	12
Periploca sepium	Apocynaceae	8.152 ± 0.068	1.820 ± 0.050	0.852 ± 0.009	5.506	Long-circular	Hair	5.852	12
Bothriochloa ischaemum	Poaceae	1.986 ± 0.085	0.744 ± 0.030	0.470 ± 0.036	0.432	Long-spindle	Awn	2.904	12
Patrinia scabiosifolia	Caprifoliaceae	2.244 ± 0.029	1.156 ± 0.024	1.110 ± 0.037	0.810	Ellipsoid	Wing	1.532	12
Linum usi- tatissimum	Linaceae	$\textbf{2.722} \pm \textbf{0.106}$	1.446 ± 0.083	0.666 ± 0.064	0.849	Long-oval	None	3.129	12
Lespedeza davurica	Fabaceae	3.238 ± 0.185	1.770 ± 0.053	1.156 ± 0.038	2.129	Obovate	None	2.166	12
Sophora davidii	Fabaceae	3.064 ± 0.038	3.992 ± 0.087	2.952 ± 0.047	23.769	Oval	None	1.195	12

Table 1. Seed morphology of the experimental species.

4.3.2. Water Potential Effects

After the end of the temperature experiment, we found that most of the seeds exhibited better germination performance at 20 °C. Therefore, we chose to evaluate the influence of water potential on germination under the temperature condition of 20 °C. In Petri dishes measuring 90mm in diameter, four seed duplicates were arranged on two filter paper sheets wetted with either a separate 10 mL PEG solution or distilled water (control). Solutions of polyethylene glycol 6000 (PEG 6000) (Hangzhou, China) were made in accordance with Michel and Kaufmann's (1973) protocols [103]. Every other day, the seeds were moved to new filter paper that contained either distilled water or a fresh solution in order to maintain relatively steady water potential during germination. The seed number settings for the species were consistent with those of the temperature-effect germination experiments. A light (12 h/12 h, daily photoperiod) was used to incubate the seeds at 20 °C with varying water potentials of -0.3, -0.6, -0.9, and -1.2 MPa. The number of germinated seeds was counted every day, and the germination period was 30 days.

4.3.3. Interactions of Temperature and Water Potential

By analyzing the temperature experiments, we found that the studied seeds had a higher germination rate between 15 and 30 °C. Therefore, this experiment set four constant temperatures (15, 20, 25, and 30 °C) and five levels of water potential (0, -0.3, -0.6, -0.9, and -1.2 MPa), resulting in twenty different treatments, to investigate the combined influence of temperature and water potential on seed germination. The number of seeds and the incubator condition settings were consistent with the above two germination experiments. The number of germinated seeds was counted every day and the germination period was 30 days.

4.4. Mathematical Models

To calculate the time process of germination changing with temperature, a thermal time model was used [42]. This model can be written as

$$\theta_{T(g)} = (T - T_b)t_g \tag{1}$$

$$GR_g = 1/t_g = (T - T_b)/\theta_{T(g)}$$
⁽²⁾

$$\theta_2 = (T_{c(g)} - T)t_g \tag{3}$$

or

$$GR_g = 1/t_g = (T_{c(g)} - T)t_g/\theta_2$$
(4)

The temperature (°C), base temperature (°C), time to achieve a specific germination percentage g (d), thermal time constant for a specific germination rate (g) in the population at a sub-optimal temperature (°C·d), thermal time constant at supra-optimal temperatures (°C·d), and ceiling temperature (°C) are represented by T, T_b , t_g , $\theta_{T(g)}$, θ_2 , and $T_{c(g)}$, respectively [29,42].

A hydrotime model (HT; Equations (5) and (6)) proposed by Gummerson (1986) was used to quantify the response of germination rate to Ψ [104]:

$$\theta_H = (\Psi - \Psi_{b(g)})t_g \tag{5}$$

or

$$GR_g = 1/t_g = (\Psi - \Psi_{b(g)})/\theta_H$$
(6)

The hydrotime constant (MPa·h), real water potential (MPa), and base water potential (MPa) or drought tolerance threshold values are represented by the variables θ_H , Ψ , and $\Psi_{b(g)}$ [10,104].

The degree of fit between the predicted and observed data was evaluated using the coefficient of determination (R^2). The fraction variance accounted for by the simulation model R^2 was calculated using Equation (7):

$$R^{2} = 1 - \sum (y_{obs} - y_{pre})^{2} / \sum (y_{obs} - \overline{y}_{obs})^{2}$$
(7)

where y_{obs} represents the observed values, y_{pre} represents the predicted values, and \overline{y}_{obs} represents the mean of the observed values. An R^2 value of 1 indicates that the model is in perfect accordance with the observations.

4.5. Statistical Analysis

All statistical analyses were conducted using SPSS 22.0, Excel 2021, and Origin 9.1 software. In both experiments, we employed one-way ANOVA to investigate the effects of temperature and water potential on the germination percentage, or rate (1/T50), for each species. The effects of species, temperature, and water potential on germination characterizations were tested using two-way ANOVA. The Duncan test was used to screen for significant differences between treatments at p < 0.05. The K-means clustering approach was utilized to determine clusters of distinct subclasses. We used a thermal time model to determine the temperature threshold for species germination and a hydrotime model to determine the base water potential for the germination of different species. Linear fitting between the observed and predicted germination rates was performed, and the coefficient of determination (R^2) was used to evaluate the goodness of fit of the model. Meanwhile, the association between seed morphological characteristics and plant responses to temperature and water potential was evaluated through the linear fitting of seed size and shape to base temperature and base water potential, respectively.

5. Conclusions

Our findings show that in most species, the percentage and pace of germination increased initially, declined with rising temperature, and subsequently dropped with falling water potential. The species had different temperature thresholds and water potential thresholds, and the thresholds changed with increasing germination percentage. In general, the base water potential for germination was negatively correlated with mean seed mass and was lower for more rounded seeds than for elongated seeds. However, a general mechanism cannot yet be generalized between temperature thresholds and either mean seed mass or FI. Each species differed in their resistance to external environmental stresses; among them, *A. sacrorum* was more resistant to low temperatures; *P. sepium* to high temperatures; and *L. davurica*, *S. davidii*, *L. usitatissmum*, *A. sacrorum*, *A. giraldii*, and *A. scoparia* to

or

drought stresses. Plants with strong resistance to high temperatures and drought can be prioritized as species for vegetation restoration in loess hilly regions. The seed germination of the nine native plant species can be accurately predicted using both the thermal and hydrotime models, which can be used to forecast how the region's flora will spread in the event of climate change. However, the limitations of this study are the relatively small number of species selected and the fact that only the effects of seed size and shape on germination thresholds were considered. Future studies should increase the number of species and consider the relationship between other seed traits (e.g., appendages and seed coat) and germination thresholds to achieve a comprehensive understanding of the limiting factors of vegetation regeneration in the region under climate change, and also to provide a theoretical basis for ecological restoration construction.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/plants13050693/s1, Figure S1: Linear regression of germination rate (1/tg) of nine species (different percentiles) and water potentials; Table S1: Estimation of cardinal temperatures for seed germination of nine species at 0 MPa using linear regression analysis at different percentiles (20–80%); Table S2: Estimation of cardinal water potential for seed germination of nine species at 20 °C using linear regression analysis at different percentiles (20–80%).

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References

- 1. Sourav, M.; Ashok, K.M. Increase in Compound Drought and Heatwaves in a Warming World. *Geophys. Res. Lett.* 2021, 48, e2020GL090617. [CrossRef]
- 2. Kumar Puran, T.; Sourav, M.; Ashok, K.M.; Michael, M.; Williams, A.P. Climate change will accelerate the high-end risk of compound drought and heatwave events. *Proc. Natl. Acad. Sci. USA* **2023**, *120*, e2219825120. [CrossRef]
- 3. Liu, M.; Qiao, N.; Zhang, B.; Liu, F.; Miao, Y.; Chen, J.; Sun, Y.; Wang, P.; Wang, D. Differential responses of the seed germination of three functional groups to low temperature and darkness in a typical steppe, Northern China. *PeerJ* 2022, 10, e14485. [CrossRef]
- 4. 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]
- Sun, G.Q.; Li, L.; Li, J.; Liu, C.; Wu, Y.P.; Gao, S.; Wang, Z.; Feng, G.L. Impacts of climate change on vegetation pattern: Mathematical modeling and data analysis. *Phys. Life Rev.* 2022, 43, 239–270. [CrossRef]
- Salete Capellesso, E.; Cequinel, A.; Marques, R.; Luisa Sausen, T.; Bayer, C.; Marques, M.C.M. Co-benefits in biodiversity conservation and carbon stock during forest regeneration in a preserved tropical landscape. *For. Ecol. Manag.* 2021, 492, 119222. [CrossRef]
- Dalgleish, H.J.; Koons, D.N.; Adler, P.B. Can life-history traits predict the response of forb populations to changes in climate variability? J. Ecol. 2010, 98, 209–217. [CrossRef]
- Gurvich, D.E.; Pérez-Sánchez, R.; Bauk, K.; Jurado, E.; Ferrero, M.C.; Funes, G.; Flores, J. Combined effect of water potential and temperature on seed germination and seedling development of cacti from a mesic Argentine ecosystem. *Flora* 2017, 227, 18–24. [CrossRef]
- Pautasso, M.; Dehnen-Schmutz, K.; Holdenrieder, O.; Pietravalle, S.; Salama, N.; Jeger, M.J.; Lange, E.; Hehl-Lange, S. Plant health and global change—Some implications for landscape management. *Biol. Rev. Camb. Philos. Soc.* 2010, *85*, 729–755. [CrossRef] [PubMed]
- Bakhshandeh, E.; Pirdashti, H.; Vahabinia, F.; Gholamhossieni, M. Quantification of the Effect of Environmental Factors on Seed Germination and Seedling Growth of Eruca (*Eruca sativa*) Using Mathematical Models. *J. Plant Growth Regul.* 2019, 39, 190–204. [CrossRef]
- 11. Jay Ram, L.; Philippe, D.; Christian, S.; Ming Pei, Y.; Martin, J.B.; Jean Noël, A. Abiotic and biotic factors affecting crop seed germination and seedling emergence: A conceptual framework. *Plant Soil* **2018**, 432, 1–28. [CrossRef]
- 12. Rouhollah, A.; Ahmadreza, M.; Sanam, G. Effect of environmental factors on seed germination and emergence of *Lepidium* vesicarium. Plant Species Biol. 2015, 31, 178–187. [CrossRef]

- 13. Ahmadi, A. The effect of temperature, salinity and soil burial on canary grass (*Phalaris minor*) germination. *Jordan J. Agric. Sci.* **2017**, *13*, 1052954.
- 14. Bao, G.; Zhang, P.; Wei, X.; Zhang, Y.; Liu, W. Comparison of the effect of temperature and water potential on the seed germination of five *Pedicularis kansuensis* populations from the Qinghai–Tibet plateau. *Front. Plant Sci.* 2022, 13, 1052954. [CrossRef] [PubMed]
- 15. Hu, X.W.; Fan, Y.; Baskin, C.C.; Baskin, J.M.; Wang, Y.R. Comparison of the effects of temperature and water potential on seed germination of Fabaceae species from desert and subalpine grassland. *Am. J. Bot.* **2015**, *102*, 649–660. [CrossRef] [PubMed]
- 16. Shah, S.Z.; Rasheed, A.; El-Keblawy, A.; Gairola, S.; Phartyal, S.S.; Gul, B.; Hameed, A. Inter-provenance variation in seed germination response of a cash crop halophyte *Suaeda fruticosa* to different abiotic factors. *Flora* 2022, 292, 152079. [CrossRef]
- Rowena, L.L.; Marta, J.G.; Michael, R.; Scott, J.K.; Louise, C.; Danica, E.G.; Lucy, C.; David, A.W.; Cherry, H.; William, E.F.-S. The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biol. Rev.* 2014, 90, 31–59. [CrossRef]
- 18. Donohue, K.; Rubio de Casas, R.; Burghardt, L.; Kovach, K.; Willis, C.G. Germination, Postgermination Adaptation, and Species Ecological Ranges. *Annu. Rev. Ecol. Evol. Syst.* **2010**, *41*, 293–319. [CrossRef]
- 19. Cheng, J.; Huang, H.; Liu, W.; Zhou, Y.; Han, W.; Wang, X.; Zhang, Y. Unraveling the Effects of Cold Stratification and Temperature on the Seed Germination of Invasive *Spartina alterniflora* across Latitude. *Front. Plant Sci.* **2022**, *13*, 911804. [CrossRef]
- Yan, A.; Chen, Z. The Control of Seed Dormancy and Germination by Temperature, Light and Nitrate. *Bot. Rev.* 2020, *86*, 39–75. [CrossRef]
- 21. Ejaz Ahmad, W.; Rashid, A.; Abdul, H.; Tariq, A. Alleviation of temperature stress by nutrient management in crop plants: A review. J. Soil Sci. Plant Nutr. 2012, 12, 221–244. [CrossRef]
- 22. Diego, B.; Roberto, L.B.-A. A framework for the interpretation of temperature effects on dormancy and germination in seed populations showing dormancy. *Seed Sci. Res.* **2015**, *25*, 147–158. [CrossRef]
- 23. Kamel, K.; Ghorbel, M.; Mohamed, C. Modeling the influence of temperature, salt and osmotic stresses on seed germination and survival capacity of *Stipa tenacissima* L. *Plant Biol.* **2023**, *157*, 325–338. [CrossRef]
- 24. Bertuzzi, T.; Pastrana-Ignes, V.; Curti, R.N.; Batlla, D.; Baskin, C.C.; Sühring, S.; Galíndez, G. Variation in thermal and hydrotime requirements for seed germination of Chaco seasonally dry forest species in relation to population environmental conditions and seed mass. *Austral Ecol.* **2022**, *47*, 1232–1247. [CrossRef]
- Sampayo-Maldonado, S.; Ordoñez-Salanueva, C.A.; Mattana, E.; Ulian, T.; Way, M.; Castillo-Lorenzo, E.; Dávila-Aranda, P.D.; Lira-Saade, R.; Téllez-Valdéz, O.; Rodriguez-Arevalo, N.I.; et al. Thermal Time and Cardinal Temperatures for Germination of *Cedrela odorata* L. *Forests* 2019, *10*, 841. [CrossRef]
- Alvarado, V.; Bradford, K.J. A hydrothermal time model explains the cardinal temperatures for seed germination. *Plant Cell Environ.* 2002, 25, 1061–1069. [CrossRef]
- 27. Hardegree, S.P.; Jones, T.A.; Van Vactor, S.S. Variability in thermal response of primed and non-primed seeds of squirreltail [*Elymus elymoides* (Raf.) Swezey and *Elymus multisetus* (J. G. Smith) M. E. Jones]. *Ann. Bot.* **2002**, *89*, 311–319. [CrossRef] [PubMed]
- Dantas, B.F.; Moura, M.S.B.; Pelacani, C.R.; Angelotti, F.; Taura, T.A.; Oliveira, G.M.; Bispo, J.S.; Matias, J.R.; Silva, F.F.S.; Pritchard, H.W.; et al. Rainfall, not soil temperature, will limit the seed germination of dry forest species with climate change. *Oecologia* 2020, 192, 529–541. [CrossRef]
- 29. Hosseini Sanehkoori, F.; Pirdashti, H.; Bakhshandeh, E. Quantifying water stress and temperature effects on camelina (*Camelina sativa* L.) seed germination. *Environ. Exp. Bot.* **2021**, *186*, 104450. [CrossRef]
- 30. Trudgill, D.L.; Squire, G.R.; Ken, T. A thermal time basis for comparing the germination requirements of some British herbaceous plants. *New Phytol.* **2000**, *145*, 107–114. [CrossRef]
- Coyne, C.J.; Kumar, S.; von Wettberg, E.J.B.; Marques, E.; Berger, J.D.; Redden, R.J.; Ellis, T.H.N.; Brus, J.; Zablatzká, L.; Smýkal, P. Potential and limits of exploitation of crop wild relatives for pea, lentil, and chickpea improvement. *Legume Sci.* 2020, 2, e36. [CrossRef]
- 32. Hatfield, J.L.; Prueger, J.H. Temperature extremes: Effect on plant growth and development. *Weather Clim. Extrem.* **2015**, *10*, 4–10. [CrossRef]
- Kamkar, B.; Jami Al-Alahmadi, M.; Mahdavi-Damghani, A.; Villalobos, F.J. Quantification of the cardinal temperatures and thermal time requirement of opium poppy (*Papaver somniferum* L.) seeds to germinate using non-linear regression models. *Ind. Crops Prod.* 2012, 35, 192–198. [CrossRef]
- Zhang, R.; Luo, K.; Chen, D.; Baskin, J.; Baskin, C.; Wang, Y.; Hu, X. Comparison of Thermal and Hydrotime Requirements for Seed Germination of Seven Stipa Species From Cool and Warm Habitats. *Front. Plant Sci.* 2020, 11, 560714. [CrossRef] [PubMed]
- Greve, P.; Roderick, M.L.; Ukkola, A.M.; Wada, Y. The aridity Index under global warming. *Environ. Res. Lett.* 2019, 14, 124006. [CrossRef]
- 36. Miguel, B.; Manuel, D.-B.; Santiago, S.; Rocío, H.-C.; Yanchuang, Z.; Juan, G.; Nicolas, G.; Hugo, S.; Vincent, M.; Anika, L.; et al. Global ecosystem thresholds driven by aridity. *Science* **2020**, *367*, 787–790. [CrossRef]
- 37. Guillén, S.; Terrazas, T.; De la Barrera, E.; Casas, A. Germination differentiation patterns of wild and domesticated columnar cacti in a gradient of artificial selection intensity. *Genet. Resour. Crop Evol.* **2010**, *58*, 409–423. [CrossRef]
- 38. Chengjie, G.; Fangyan, L.; Chunhua, Z.; Defeng, F.; Kun, L.; Kai, C. Germination responses to water potential and temperature variation among provenances of Pinus yunnanensis. *Flora* **2021**, 276–277, 151786. [CrossRef]

- Martínez-López, M.; Tinoco-Ojanguren, C.; Martorell, C. Drought tolerance increases with seed size in a semiarid grassland from southern Mexico. *Plant Ecol.* 2020, 221, 989–1003. [CrossRef]
- 40. Souza, C.S.; Ramos, D.M.; Barbosa, E.R.M.; Borghetti, F. Germination of grass species from dry and wet grasslands in response to osmotic stress under present and future temperatures. *Am. J. Bot.* **2022**, *109*, 2018–2029. [CrossRef]
- 41. Bradford, K.J. A Water Relations Analysis of Seed Germination Rates. Plant Physiol. 1990, 94, 840–849. [CrossRef]
- 42. Kent, J.B. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. *Weed Sci.* 2002, *50*, 248–260. [CrossRef]
- 43. Esmaeil, B.; Ali Jabraeil, J.M. Population-based threshold models: A reliable tool for describing aged seeds response of rapeseed under salinity and water stress. *Environ. Exp. Bot.* 2020, *176*, 104077. [CrossRef]
- 44. Romano, A.; Bravi, R. Hydrotime model to evaluate the effects of a set of priming agents on seed germination of two leek cultivars under water stress. *Seed Sci. Technol.* **2021**, *49*, 159–174. [CrossRef]
- 45. Edson, S.; Massanori, T.; Victor José Mendes, C. Germination response of *Hylocereus setaceus* (Salm-Dyck ex DC:) Ralf Bauer (Cactaceae) seeds to temperature and reduced water potentials. *Braz. J. Biol.* **2010**, *70*, 135–144. [CrossRef]
- 46. Han, C.; Yang, P. Studies on the molecular mechanisms of seed germination. Proteomics 2015, 15, 1671–1679. [CrossRef]
- 47. D'Aguillo, M.C.; Edwards, B.R.; Donohue, K. Can the Environment have a Genetic Basis? A Case Study of Seedling Establishment in *Arabidopsis thaliana*. J. Hered. 2019, 110, 467–478. [CrossRef]
- 48. Nur, M.; Baskin, C.C.; Lu, J.J.; Tan, D.Y.; Baskin, J.M. A new type of non-deep physiological dormancy: Evidence from three annual Asteraceae species in the cold deserts of Central Asia. *Seed Sci. Res.* **2014**, *24*, 301–314. [CrossRef]
- 49. Veselá, A.; Duongová, L.; Münzbergová, Z. Plant origin and trade-off between generative and vegetative reproduction determine germination behaviour of a dominant grass species along climatic gradients. *Flora* **2022**, 297, 152177. [CrossRef]
- 50. Bakhshandeh, E.; Jamali, M. Halothermal and hydrothermal time models describe germination responses of canola seeds to ageing. *Plant Biol.* **2021**, *23*, 621–629. [CrossRef]
- 51. Alinia, M.; Jalali, A.H.; Kazemeini, S.A.; Bakhshandeh, E. Modeling seed germination response of maize with different shapes and sizes using halotime and halothermal time concept. *Acta Physiol. Plant.* **2022**, *44*, 133. [CrossRef]
- Ambika, S.; Manonmani, V.; Somasundar, G. Review on Effect of Seed Size on Seedling Vigour and Seed Yield. *Res. J. Seed Sci.* 2014, 7, 31–38. [CrossRef]
- 53. Gremer, J.R.; Venable, D.L. Bet hedging in desert winter annual plants: Optimal germination strategies in a variable environment. *Ecol. Lett.* **2014**, *17*, 380–387. [CrossRef] [PubMed]
- 54. Susko, D.J.; Cavers, P.B. Seed size effects and competitive ability in *Thlaspi arvense* L. (Brassicaceae). *Botany* **2008**, *86*, 259–267. [CrossRef]
- 55. Wang, G.; Lynch, A.L.; Cruz, V.M.V.; Heinitz, C.C.; Dierig, D.A. Temperature requirements for guayule seed germination. *Ind. Crops Prod.* 2020, 157, 112934. [CrossRef]
- 56. Liu, Y.; Hou, X.; Qiao, J.; Zhang, W.; Fang, M.; Lin, M. Evaluation of soil erosion rates in the hilly-gully region of the Loess Plateau in China in the past 60 years using global fallout plutonium. *Catena* **2023**, *220*, 106666. [CrossRef]
- 57. Jia, X.X.; Shao, M.A.; Zhu, Y.J.; Luo, Y. Soil moisture decline due to afforestation across the Loess Plateau, China. J. Hydrol. 2017, 546, 113–122. [CrossRef]
- Zhang, Y.; Feng, T.; Wang, L.; Wang, X.; Wei, T.; Wang, P. Effects of long-term vegetation restoration on soil physicochemical properties mainly achieved by the coupling contributions of biological synusiae to the Loess Plateau. *Ecol. Indic.* 2023, 152, 110353. [CrossRef]
- 59. Huang, L.; Zhao, W.; Shao, M.A. Response of plant physiological parameters to soil water availability during prolonged drought is affected by soil texture. *J. Arid. Land* **2021**, *13*, 688–698. [CrossRef]
- 60. Hu, J.; Li, K.; Deng, C.; Gong, Y.; Liu, Y.; Wang, L. Seed Germination Ecology of Semiparasitic Weed *Pedicularis kansuensis* in Alpine Grasslands. *Plants* **2022**, *11*, 1777. [CrossRef]
- 61. Zaferanieh, M.; Batool, M.; Benjamin, T. Effect of temperature and water potential on *Alyssum homolocarpum* seed germination: Quantification of the cardinal temperatures and using hydro thermal time. *S. Afr. J. Bot.* **2020**, *131*, 259–266. [CrossRef]
- 62. Allison, R.K. Regulatory mechanisms involved in the transition from seed development to germination. *Crit. Rev. Plant Sci.* **1990**, *9*, 155–195. [CrossRef]
- 63. Luis, S.-L.; Marina, G.-R.; David, D.-P.; Fernando, G.-C.; Viridiana, C.-A.; Viridiana, Z.-V.; Viridiana, L.-L.; Rafael, M.-S.; Irma, B.-L.; Sobeida, S.-N. Early carbon mobilization and radicle protrusion in maize germination. *J. Exp. Bot.* **2012**, *63*, 4513–4526. [CrossRef]
- 64. Kazım, M.; Demir, I.; Matthews, S. Mean germination time estimates the relative emergence of seed lots of three cucurbit crops under stress conditions. *Seed Sci. Technol.* **2010**, *38*, 14–25. [CrossRef]
- 65. Badano, E.I.; Sánchez-Montes de Oca, E.J. Seed fate, seedling establishment and the role of propagule size in forest regeneration under climate change conditions. *For. Ecol. Manag.* **2022**, *503*, 119776. [CrossRef]
- Haj Sghaier, A.; Khaeim, H.; Tarnawa, Á.; Kovács, G.P.; Gyuricza, C.; Kende, Z. Germination and Seedling Development Responses of Sunflower (*Helianthus annuus* L.) Seeds to Temperature and Different Levels of Water Availability. *Agriculture* 2023, 13, 608. [CrossRef]
- 67. Sharma, P.; Sharma, M.M.M.; Patra, A.; Vashisth, M.; Mehta, S.; Singh, B.; Tiwari, M.; Pandey, V. Influence of high-temperature stress on rice growth and development—A review. *Heliyon* **2022**, *8*, 123–152. [CrossRef]

- 68. Pankaj, S.; Mayur Mukut Murlidhar, S.; Anupam, P.; Medhavi, V.; Sahil, M.; Singh, B.M.; Manish, T.; Vimal, P. *The Role of Key Transcription Factors for Cold Tolerance in Plants*; Elsevier: Amsterdam, The Netherlands, 2020. [CrossRef]
- 69. Wei, L.N.; Zhang, C.P.; Dong, Q.M.; Yang, Z.Z.; Chu, H.; Yu, Y.; Yang, X.X. Effects of temperature and water potential on seed germination of 13 *Poa* L. species in the Qinghai-Tibetan Plateau. *Glob. Ecol. Conserv.* **2021**, *25*, e01442. [CrossRef]
- 70. Khan, W.; Shah, S.; Ullah, A.; Ullah, S.; Amin, F.; Iqbal, B.; Ahmad, N.; Abdel-Maksoud, M.A.; Okla Mk El-Zaidy, M.; Al-Qahtani, W.H.; et al. Utilizing hydrothermal time models to assess the effects of temperature and osmotic stress on maize (*Zea mays* L.) germination and physiological responses. *BMC Plant Biol.* 2023, 23, 414. [CrossRef] [PubMed]
- 71. Xu, J.; Du, G. Seed germination response to diurnally alternating temperatures: Comparative studies on alpine and subalpine meadow populations. *Glob. Ecol. Conserv.* 2023, 44, e02503. [CrossRef]
- 72. de Lima, C.F.F.; Kleine-Vehn, J.; Kleine-Vehn, J.; Feraru, E. Getting to the root of belowground high temperature responses in plants. *J. Exp. Bot.* **2021**, *72*, 7404–7413. [CrossRef]
- 73. Mahtab, N.; Arash, M.; Hoseine, S.M.B. The evaluation response of onion (*Allium cepa*) seed germination to temperature by Thermal-time analysis and determine cardinal temperatures by using nonlinear regression. *J. Crop Sci.* **2017**, *48*, 961–971. [CrossRef]
- 74. Farahinia, P.; Sadat-Noori, S.A.; Mortazavian, M.M.; Soltani, E.; Foghi, B. Hydrotime model analysis of *Trachyspermum ammi* (L.) Sprague seed germination. *J. Appl. Res. Med. Aromat. Plants* **2017**, *5*, 88–91. [CrossRef]
- Luis, M.-M.; Clare, C.; Lucy, C.; Shane, R.T.; Wolfgang, L.; Jason, C.S. Interactions between seed functional traits and burial depth regulate germination and seedling emergence under water stress in species from semi-arid environments. *J. Arid. Environ.* 2017, 147, 25–33. [CrossRef]
- 76. Seyed Farhad, S.; Shirmohamadi-Aliakbarkhani, Z. Quantifying seed germination response of melon (*Cucumis melo* L.) to temperature and water potential: Thermal time, hydrotime and hydrothermal time models. S Afr. J. Bot. 2020, 130, 240–249. [CrossRef]
- 77. Cochrane, A.; Hoyle, G.L.; Yates, C.J.; Wood, J.; Nicotra, A.B. Predicting the impact of increasing temperatures on seed germination among populations of Western Australian Banksia (Proteaceae). *Seed Sci. Res.* **2014**, *24*, 195–205. [CrossRef]
- Trudgill, D.L.; Perry, J.N. Thermal time and ecological strategies—A unifying hypothesis. Ann. Appl. Biol. 1994, 125, 521–532.
 [CrossRef]
- 79. Trudgill, D.L.; Honek, A.; Li, D.; Straalen, N.M. Thermal time—Concepts and utility. Ann. Appl. Biol. 2005, 146, 1–14. [CrossRef]

80. Stevens, N.; Seal, C.E.; Archibald, S.; Bond, W. Increasing temperatures can improve seedling establishment in arid-adapted savanna trees. *Oecologia* **2014**, *175*, 1029–1040. [CrossRef] [PubMed]

- Hu, X.; Wang, J.; Wang, Y. Thermal time model analysis for seed germination of four Vicia species. *Chin. J. Plant Ecol.* 2012, 36, 841–848. [CrossRef]
- 82. López, A.S.; López, D.R.; Arana, M.V.; Batlla, D.; Marchelli, P. Germination response to water availability in populations of Festuca pallescens along a Patagonian rainfall gradient based on hydrotime model parameters. *Sci. Rep.* **2021**, *11*, 10653. [CrossRef]
- Čanak, P.; Jeromela, A.M.; Vujošević, B.; Kiprovski, B.; Mitrović, B.; Alberghini, B.; Facciolla, E.; Monti, A.; Zanetti, F. Is Drought Stress. Tolerance Affected by Biotypes and Seed Size in the Emerging Oilseed Crop Camelina? *Agronomy* 2020, 10, 1856. [CrossRef]
- 84. Bellie, S. Global climate change and its impacts on water resources planning and management: Assessment and challenges. *Stoch. Environ. Res. Risk Assess.* **2010**, *25*, 583–600. [CrossRef]
- 85. Rosbakh, S.; Phartyal, S.S.; Poschlod, P. Seed germination traits shape community assembly along a hydroperiod gradient. *Ann. Bot.* **2019**, *125*, 67–78. [CrossRef] [PubMed]
- 86. Huang, Z.; Liu, S.; Bradford, K.J.; Huxman, T.E.; Venable, D.L. The contribution of germination functional traits to population dynamics of a desert plant community. *Ecology* **2016**, *97*, 250–261. [CrossRef]
- 87. Soares da Mota, L.A.; Garcia, Q.S. Germination patterns and ecological characteristics of Vellozia seeds from high-altitude sites in south-eastern Brazil. *Seed Sci. Res.* 2013, 23, 67–74. [CrossRef]
- 88. Arène, F.; Affre, L.; Doxa, A.; Saatkamp, A. Temperature but not moisture response of germination shows phylogenetic constraints while both interact with seed mass and lifespan. *Seed Sci. Res.* **2017**, *27*, 110–120. [CrossRef]
- 89. Antoine, G.; Françoise, C.; Marie-Hélène, W.; Carolyne, D. How do seed and seedling traits influence germination and emergence parameters in crop species? A comparative analysis. *Seed Sci. Res.* **2016**, *26*, 317–331. [CrossRef]
- 90. Taylor, A.G. Seed Storage, Germination, Quality, and Enhancements; CABI eBooks: Wallingford, UK, 2020. [CrossRef]
- 91. Westoby, M.; Jurado, E.; Leishman, M. Comparative evolutionary ecology of seed size. *Trends Ecol. Evol.* **1992**, *7*, 368–372. [CrossRef]
- 92. Grossnickle, S.C.; MacDonald, J.E. Why seedlings grow: Influence of plant attributes. New Forests 2017, 49, 1–34. [CrossRef]
- 93. Wang, D.; Jiao, J.; Lei, D.; Wang, N.; Du, H.; Jia, Y. Effects of seed morphology on seed removal and plant distribution in the Chinese hill-gully Loess Plateau region. *Catena* **2013**, *104*, 144–152. [CrossRef]
- 94. Liang, Y.; Gao, G.; Li, J.; Dunkerley, D.; Fu, B. Runoff and soil loss responses of restoration vegetation under natural rainfall patterns in the Loess Plateau of China: The role of rainfall intensity fluctuation. *Catena* **2023**, 225, 107013. [CrossRef]
- 95. Song, Y.; Gao, X. Effects of low temperature and nitrogen addition during cold stratification on seed germination of Korean pine (*Pinus koraiensis*). *Can. J. For. Res.* **2021**, *51*, 1698–1706. [CrossRef]
- 96. Li, L.; Chen, J.; Han, X.; Zhang, W.; Shao, C. Shrubby Steppe Ecosystem. Ecosyst. China 2020, 2, 339–364. [CrossRef]

- 97. Wang, P.; Su, X.; Zhou, Z.; Wang, N.; Liu, J.; Zhu, B. Differential effects of soil texture and root traits on the spatial variability of soil infiltrability under natural revegetation in the Loess Plateau of China. *Catena* **2023**, 220, 106693. [CrossRef]
- Li, W.; Ma, X.; Ma, N.; Zhao, Y.; Qiao, Y.; Wang, P.; Sun, H. Effects of Grazing Intensity on Stoichiomerty of Biological Soil Crusts in the Hilly Loess Plateau region. *Acta Agrestia Sin.* 2021, 29, 2547–2555.
- 99. Silveira, F.A.O.; Fernandes, G.W. Effect of light, temperature and scarification on the germination of *Mimosa foliolosa* (Leguminosae) seeds. *Seed Sci. Technol.* 2006, 34, 585–592. [CrossRef]
- 100. Wang, D. Seed Life-History Strategies of Plants and Restoration by Seed Addition in the Hill-Gully Loess Plateau Region. Ph.D. Thesis, Northwest A&F University, Xianyang, China, 2015.
- 101. Poesen, J. Transport of rock fragments by rill flow-a field study. Catena 1987, 8, 35-54.
- 102. García-Fayos, P.; Bochet, E.; Artemi, C. Seed removal susceptibility through soil erosion shapes vegetation composition. *Plant Soil* **2010**, *334*, 289–297. [CrossRef]
- 103. Michel, B.E.; Kaufmann, M.R. The Osmotic Potential of Polyethylene Glycol 6000. Plant Physiol. 1973, 51, 914–916. [CrossRef]
- 104. Gummerson, R.J. The Effect of Constant Temperatures and Osmotic Potentials on the Germination of Sugar Beet. J. Exp. Bot. 1986, 37, 729–741. [CrossRef]

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