Seed Germination Characteristics and Geographical Variation of Six Catalpa Provenances under Simulated Drought Stress (Postprint)

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Abstract

This study employed polyethylene glycol (PEG-6000) to simulate drought stress and measured indicators including germination rate, germination potential, and radicle length. Correlation analysis, cluster analysis, and membership function method were utilized to comprehensively evaluate the drought resistance of seeds from six provenances of Catalpa ovata during germination, preliminarily screening provenances with superior drought resistance. The objective was to select elite rootstock for grafting propagation of Catalpa bungei in China, thereby promoting improved variety breeding and establishing a material foundation for large-scale application. The results demonstrated that with decreasing solution water potential, germination rate, germination potential, relative germination rate, germination index, and vigor index of seeds from all six provenances exhibited continuous decline. Except for radicle and hypocotyl lengths in the Henan Luoyang provenance and radicle length in the Gansu Zhengning provenance, all other provenances showed gradual decreases in radicle and hypocotyl lengths. At a solution water potential of -1.0 MPa, the Henan Luoyang provenance became inactive, while indicators of remaining provenances converged. Correlation analysis between seed germination characteristics and geographical environmental factors of provenances indicated that seed vigor index was significantly positively correlated with longitude and latitude (0.903 and 0.871, respectively); provenances at higher longitude and latitude exhibited stronger vigor and superior drought resistance. Higher annual mean temperature decreased seed germination rate and vigor. Annual rainfall showed moderately weak negative correlation with seed germination rate and vigor index, but moderate positive correlation with radicle and hypocotyl growth. Temperature and rainfall influenced drought resistance of Catalpa ovata seeds, primarily manifested as lower germination rates corresponding to lower annual mean temperature and rainfall. Preliminary findings indicated that Catalpa ovata provenances from harsh environments (arid and cold regions) exhibited a regulatory mechanism adapting to

adverse conditions by elevating seed germination rate while reducing embryonic growth activity. Given limitations of correlation analysis, cluster analysis and membership function method were employed for comprehensive evaluation of drought resistance during germination of the six provenances. The Liaoning Hengren provenance demonstrated strongest seed drought resistance, whereas Henan Luoyang provenance exhibited the weakest. In conclusion, significant differences in drought resistance existed among the six Catalpa ovata provenances, with temperature and rainfall influencing drought resistance of seed germination to a certain degree.

Full Text

Abstract

This study employed polyethylene glycol (PEG-6000) to simulate drought stress and measured indicators including germination percentage, germination potential, and radicle length. Correlation analysis, cluster analysis, and membership function methods were used to comprehensively evaluate the drought resistance of seeds from six Catalpa ovata provenances during germination, with the aim of initially screening for provenances with stronger drought resistance to serve as superior rootstocks for Catalpa bungei grafting propagation in China. This would promote improved variety breeding and lay a material foundation for large-scale application. The results showed that as solution water potential decreased, the germination percentage, germination potential, relative germination percentage, germination index, and vigor index of seeds from all six provenances exhibited a continuous declining trend. Except for radicle and hypocotyl length in the Luoyang, Henan provenance and radicle length in the Zhengning, Gansu provenance, the radicle and hypocotyl lengths of other provenances showed a gradual decreasing trend. At a solution water potential of -1.0 MPa, the Luoyang, Henan provenance became inactive, while indicators for the remaining provenances tended to converge. Correlation analysis between seed germination characteristics and geographical environmental factors at the origin revealed that seed vigor index was significantly positively correlated with longitude and latitude (0.903 and 0.871, respectively), with provenances from higher latitudes and longitudes showing greater vigor and better drought resistance. Higher mean annual temperatures reduced both seed germination percentage and vigor. Annual rainfall showed a moderately weak negative correlation with seed germination percentage and vigor index, but a moderate positive correlation with radicle and hypocotyl growth. Temperature and precipitation affected the drought resistance of C. ovata seeds, primarily manifested as lower germination percentages under lower mean annual temperatures and precipitation. Preliminary findings indicated that provenances from relatively harsh environments characterized by drought and cold exhibited an adaptive mechanism of increasing seed germination percentage while reducing embryo growth activity. Given the limitations of correlation analysis, cluster analysis and membership function methods were applied for comprehensive drought resistance evaluation,

revealing that the Hengren, Liaoning provenance showed the strongest drought resistance, while the Luoyang, Henan provenance showed the weakest. In summary, significant differences in drought resistance existed among the six C. ovata provenances, with temperature and rainfall influencing drought resistance during seed germination to a certain extent.

Keywords: Catalpa ovata, provenance, PEG stress, seed germination, drought resistance

Introduction

Grafting is an effective measure for clonal propagation and has been widely applied in plant breeding. Beyond grafting methods, the compatibility between rootstock and scion is a key factor affecting scion growth. Recent studies have demonstrated that rootstock type influences the growth and stress resistance of grafted seedlings. Wang et al. (2008) found that grafted seedlings with golden catalpa rootstock exhibited enhanced resistance in C. bungei, significantly outperforming self-rooted seedlings and those grafted with Catalpa fargesii rootstock. Sun et al. (2010) showed that among three rootstock types—golden melon, Chinese pumpkin, and bottle gourd—bottle gourd as rootstock significantly improved nutrient content in watermelon leaves. Additional reports have confirmed that appropriate rootstock types effectively improve scion drought resistance (Li et al., 2018), salt tolerance (Podda et al., 2017), cold resistance (Li et al., 2017), and waterlogging tolerance (Tang et al., 2016). Thus, selecting suitable rootstock can substantially improve various resistance indicators in scions.

Catalpa bungei is an ancient, high-quality precious timber and ornamental tree species native to China (Cen, 2008). However, due to low rooting rates of hardwood cuttings (Yang et al., 2014), propagation primarily relies on bud grafting. Catalpa ovata, a congeneric species, possesses characteristics including well-developed root systems and strong stress resistance, and demonstrates good compatibility with C. bungei scions. Consequently, C. bungei grafting has traditionally employed C. ovata rootstock (Wang et al., 2008; Chen et al., 2007). Currently, China produces over 10 million C. bungei grafted seedlings annually, widely used in national reserve forests, urban landscaping, and corridor greening projects. However, large-scale grafting propagation has encountered new challenges, including compatibility between C. ovata provenances and C. bungei varieties and differential resistance among C. ovata provenances, which have affected production and application of C. bungei grafted seedlings to some extent. Therefore, evaluating resistance in C. ovata provenances represents an effective approach to expanding C. bungei application scope and improving improved variety utilization.

The seed germination stage is both a critical period in plant life history and an important indicator for assessing drought resistance, directly determining subsequent plant growth (Li et al., 2010). Research has shown that seed drought

resistance correlates highly with seedling drought resistance (Yu et al., 1997; Wang et al., 2014; Ji et al., 2017), and differences in seed germination among provenances may result from factors including altitude, latitude/longitude, and climate (Herrera, 1991; Matthies, 1990; Brad et al., 2004). This study selected seeds from six C. ovata provenances for PEG-simulated drought stress treatment, analyzing the effects of PEG stress on germination and seedling growth of different provenances and evaluating differences in drought resistance to support breeding and promotion of superior C. bungei grafted seedlings.

Materials and Methods

1.1 Experimental Materials

In 2014, seeds were collected from six counties (cities/districts) in six provinces within the main distribution area of C. ovata. At each collection site, seeds were harvested from 10 mother trees with straight stems, good growth, and no pest or disease damage, at normal flowering and fruiting age. Mother trees were spaced at least 100 m apart linearly. Seeds collected from the same site were mixed uniformly as the experimental provenance material. Provenance numbers, geographical locations, and climatic conditions are shown in Table 1 .

1.2 Experimental Design

Different concentrations of PEG-6000 solution were used to simulate drought stress, with solution water potential serving as the metric for drought severity. Four gradients were established: 0.0 MPa (CK), -0.5 MPa, -1.0 MPa, and -1.7 MPa, with four replicates per treatment and 100 seeds per replicate.

1.2.1 Seed Pretreatment One day before sowing, seeds from each provenance were disinfected with 5‰ potassium permanganate solution for 1 hour, rinsed clean with tap water, and soaked in water at an initial temperature of 40°C (allowed to cool naturally) for 24 hours.

1.2.2 Sowing and Drought Stress Treatment According to the experimental design, filter paper was moistened with PEG solutions of different water potentials. Two layers of treated filter paper were placed at the bottom of each petri dish, and seeds were arranged neatly on the filter paper. The solution height in the petri dish reached one-third of seed thickness, with the control group (CK) cultivated with distilled water. Each petri dish was weighed using an electronic balance (precision 0.01 g) and numbered.

1.2.3 Culture Conditions Seeds under different PEG treatments were placed in an illuminated incubator (HPG-280BX) for cultivation. Light conditions: fluorescent light intensity 150 $mol \cdot m^{-2} \cdot s^{-1}$, 28°C, 8:00–18:00; Dark conditions: 22°C, 18:00–8:00.

1.3 Measurements

1.3.1 Seed Germination Investigation Following treatment, the number of germinated seeds was observed and recorded daily. The germination standard was defined as radicle length equal to seed length and plumule length equal to half of seed length (Li and Xu, 1989). Germination counts were recorded daily at fixed times, and the investigation was terminated when no additional seeds germinated for two consecutive weeks.

1.3.2 Seedling Measurement On day 12 of C. ovata seed cultivation, radicle and hypocotyl lengths of germinated seeds were measured with 0.1 cm precision. Ten uniformly growing seedlings were selected from each replicate under each treatment for measurement.

1.4 Index Measurement and Data Analysis

Excel 2010 and SPSS 22.0 were used for data processing, statistical analysis, and graph production. ANOVA was employed to test for significant differences in seed traits and seedling growth among different provenances, with Duncan' s multiple comparison method applied.

Specific calculation formulas for relevant growth indicators were as follows:

Germination percentage G = (n/N) × 100%, where n is the number of germinated seeds and N is the total number of seeds in the sample (Sun, 1992).

Relative germination percentage = (G /G) × 100%, where G is seed germination percentage under treatment and G is germination percentage of the control.

Germination potential = (Number of germinated seeds during peak germination period, generally counted within the first 1/3 of days) / Total number of tested seeds × 100%.

Germination index: Gi = Σ(Gt/Dt), where Gt is the number of germinated seeds on day t and Dt is the corresponding germination day (Zheng, 2004).

Vigor index: Iv = s × Gi, where s is fresh seedling weight (Zheng, 2004).

1.5 Comprehensive Drought Resistance Evaluation Method

The fuzzy membership function method was employed for comprehensive drought resistance evaluation (Li et al., 2010; Ren et al., 2013). To reasonably assess the sensitivity of different C. ovata provenances to PEG stress, the critical water potential value for seed germination was used as an evaluation indicator. Membership function values for each indicator were calculated using the following formulas: Formula (1) was applied when the indicator was positively correlated with drought resistance, and Formula (2) when negatively correlated.

Where: (Xij) is the membership function value of indicator j for provenance i, Xij is the value of indicator j for provenance i, Xjmax is the maximum value of indicator j among all provenances, and Xjmin is the minimum value of indicator j.

Results

2.1 Effects of Drought Stress on Germination Characteristics of Different C. ovata Provenances

Figure 1 [Figure 1: see original paper] shows that the HEN provenance exhibited significantly lower germination than other provenances under all stress treatments. At water potentials of 0 and -0.5 MPa, the LN provenance showed significantly higher germination percentage than other provenances (Figure 2 [Figure 2: see original paper]A), while no significant differences were observed among HB, HN, and GS provenances at each water potential, with GZ and HEN provenances showing significantly lower germination percentages than others. At -1.0 MPa water potential, germination of all six provenances was significantly inhibited, with HEN provenance germination approaching zero and the remaining five provenances maintaining low germination percentages. At -1.7 MPa water potential, only the GS provenance showed low germination percentage, with the other five provenances essentially reaching zero germination.

Regarding relative germination percentage (Figure 2B), the HEN provenance showed the greatest decline, being significantly lower than the other five provenances at -1.0 MPa water potential. Under -1.7 MPa stress, the GS provenance demonstrated significantly higher relative germination percentage than other provenances, with the remaining five approaching zero. Based on germination percentage and relative germination percentage, LN and GS provenances showed stronger drought resistance.

Table 2 results indicate that germination potential of tested seeds gradually decreased with increasing PEG stress, suggesting delayed peak germination periods under PEG drought stress, though different provenances responded differently. GS, HB, and LN provenances generally maintained high germination potential, while HN, HEN, and GZ provenances showed lower potential. The LN provenance exhibited the greatest decline, decreasing by 74.75% compared with the control. At -0.5 MPa water potential, HEN provenance germination potential was significantly lower than others at only 0.50%. At -1.0 MPa, only HB and GZ provenances showed germination potential of 1.00% and 0.25%, respectively, with other provenances reaching zero, indicating relatively greater drought potential in HB and GZ.

As shown in Figure 3 [Figure 3: see original paper], the LN provenance exhibited the highest germination index at water potentials of 0 and -0.5 MPa (mild stress), but showed a substantial decrease at -1.0 MPa. HB, GS, and HN provenances showed smaller decreases in germination index with decreasing water potential, maintaining relatively high levels, suggesting potential drought resis-

tance in these three provenances. All six provenances showed similar trends in germination index with increasing drought stress severity.

The vigor index, which reflects germination time uniformity and seedling quality, serves as a comprehensive indicator of seedling emergence capacity under stress conditions (Chen et al., 2016). With decreasing water potential, the six provenances showed different declining trends in seed vigor index (Figure 4 [Figure 4: see original paper]). GS and HEN provenances declined most rapidly under mild stress (-0.5 MPa), while the other four provenances showed consistent downward trends. GS and GZ provenances experienced a plateau period during decline, whereas the other four were significantly inhibited. Among the six provenances, LN showed the greatest decrease in vigor index, while HEN lost viability at -1.0 MPa water potential, indicating that GS and GZ provenances maintained stronger seed vigor under certain drought stress levels.

2.2 Effects of Drought Stress on Seedling Growth of Different C. ovata Provenances

Table 3 results show that HEN provenance radicle and hypocotyl lengths were significantly lower than other provenances at 0 MPa water potential, indicating low seed growth vigor that may affect subsequent seedling growth. Under control conditions, GZ and HB provenances showed significantly higher primary root lengths than the other four provenances, with no significant differences among GS, HN, and LN provenances, all significantly higher than HEN. At -1.0 MPa water potential, GZ and HB provenances maintained significantly higher primary root lengths than LN and HN, demonstrating stronger post-germination growth vigor.

The growth rate of hypocotyls in different drought-resistant C. ovata types represents an important indicator for identifying drought resistance capacity. Under control conditions, only HEN provenance hypocotyl length was significantly lower than the other five provenances. At -0.5 MPa water potential, hypocotyl lengths of all provenances were significantly inhibited without significant differences among them. At -1.0 MPa, GS, HB, and GZ provenances showed significantly higher hypocotyl lengths than LN and HN provenances, with HB showing the most pronounced inhibition. Based on radicle and hypocotyl growth, HEN provenance exhibited the weakest drought resistance.

2.3 Correlation Analysis Between Seed Indicators and Geographic-Climatic Factors

Plants within different regions of their distribution range gradually develop different genetic structures through natural selection due to differences in geographic-climatic conditions and varied plant responses, resulting in geographical variation (Xu, 1992). Correlation analysis between various provenance indicators and their corresponding geographic-climatic factors revealed that, except for radicle and hypocotyl lengths, the remaining five indicators

showed negative correlations with altitude and mean annual temperature, and positive correlations with geographic latitude and longitude. Notably, seed vigor index showed significant positive correlations with longitude and latitude, with correlation coefficients reaching 0.903 and 0.871, respectively. The general trend indicated increasing sensitivity of seed germination to drought stress with increasing altitude and mean annual temperature (Table 4).

Analysis with climatic factors showed that provenances from lower mean annual temperatures exhibited greater sensitivity of seed germination to drought stress, showing strong negative correlations with germination percentage (-0.689) and germination potential (-0.623). Annual rainfall showed moderate positive correlation with radicle and hypocotyl lengths, indicating that adequate moisture at the provenance origin enabled stronger embryo growth. Additionally, longer frost-free periods within certain ranges improved post-germination seedling growth, possibly reflecting altered genetic effects from environmental conditions.

2.4 Comprehensive Drought Resistance Evaluation of Different C. ovata Provenances

Plant drought resistance mechanisms constitute a complex system, and seed germination involves complex physiological and biochemical processes. Single indicators are insufficient for evaluating plant drought resistance, necessitating comprehensive judgment using multiple indicators (Li et al., 2010). Data from the -1.0 MPa PEG water potential treatment were selected for fuzzy membership function evaluation of germination percentage, germination potential, relative germination percentage, germination index, vigor index, radicle length, and hypocotyl length for the six C. ovata provenances. The total mean membership function values were calculated and ranked (Table 5). The LN provenance showed the highest comprehensive membership function value at 0.866, indicating the strongest drought resistance, while HEN provenance showed the weakest.

For comprehensive analysis of drought stress sensitivity among different provenances, cluster analysis was performed using Euclidean distance, with results shown in Figure 5 [Figure 5: see original paper]. The six provenances were grouped into three clusters: LN, HN, and GS provenances formed one cluster with relatively strong drought resistance, characterized by maintaining higher germination percentages and potentials under stress. HB and GZ provenances formed another cluster with intermediate drought resistance, distinguished by extremely strong radicle and hypocotyl growth capacity, possibly because genetic material in these provenances primarily regulated seed growth while genes triggering germination expression were relatively weak. HEN provenance formed a separate cluster with the poorest germination and growth indicators, showing the weakest drought resistance among the six provenances.

Discussion and Conclusion

Plant responses to drought stress depend on environmental conditions and the duration and intensity of water stress (Dale, 1988). Mother trees of different provenances within the same species develop genetic variations to adapt to local environmental changes, reflecting stable heritable traits in various seed characteristics. Consequently, seed quality and seedling growth traits vary among provenances of the same species (Yang et al., 2016). This study demonstrated significant differences in germination percentage and post-germination growth among C. ovata provenances.

The seed germination stage is a crucial period for assessing plant drought resistance, with water being a key factor affecting seed quality and germination (Chamorro et al., 2016). Using germination percentage alone as a seed quality indicator has substantial limitations, as it only reflects germination under optimal conditions without indicating seedling quality or growth vigor. Combining germination potential, relative germination percentage, germination index, and other indicators can simultaneously reflect germination capacity, uniformity, and seedling quality (Guan and Wang, 2011). PEG-simulated drought stress induced drought responses in C. ovata seeds, with germination percentage decreasing continuously as water potential declined, consistent with findings from Yu et al. (2010) on Ammopiptanthus nanus seeds under different PEG concentrations. At -1.0 MPa water potential, all six C. ovata provenances showed significant inhibition of germination indicators, with the Luoyang, Henan provenance losing viability, while at -1.7 MPa, seeds from all provenances were essentially completely inhibited, indicating that -1.0 MPa represents the critical threshold for C. ovata seed germination. The Henan provenance showed weak germination percentage, vigor index, germination index, and post-germination embryo development even under normal water conditions. The complex causes of this phenomenon require further investigation through anatomical observation of embryo development, as this study lacked morphological exploration of embryo development differences.

Significant differences existed among the six provenances in germination and seedling growth responses to drought stress. Correlation analysis between geographic-climatic factors and provenance germination characteristics revealed significant positive correlations between seed vigor index and latitude/longitude, indicating that C. ovata seed germination and growth follow a geographical variation pattern dependent on latitude and longitude. Wei et al. (2008, 2009) reported that mother trees from provenances in regions with suitable temperatures and abundant annual rainfall did not experience stress during the growing season and thus did not develop corresponding defense mechanisms against drought stress. Conversely, provenances from arid, high-temperature regions had developed specific response mechanisms under adverse conditions that formed stable heritable effects transmitted through seeds. Comprehensive correlation analysis and germination/embryo growth data under stress conditions revealed that C. ovata seeds from environmentally harsh provenances

showed higher germination percentages but weaker embryo growth activity, representing a potential drought adaptation mechanism that enhances survival rates. This study identified the Hengren, Liaoning provenance as having the strongest drought resistance through cluster analysis and fuzzy membership function evaluation, providing a material foundation for large-scale breeding of superior C. bungei grafted seedlings.

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Note: Figure translations are in progress. See original paper for figures.