Recalcitrance of Quercus wutaishanica Seeds: Dehydration and Low Temperature Sensitivity Postprint

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Abstract

Using silica gel (rapid dehydration) and a 35 ℃ electronic constant-temperature drying oven (slow dehydration), as well as cold storage (4 ℃) and frozen storage (-4 ℃), we investigated the dehydration and low-temperature sensitivity of Quercus liaotungensis seeds and their effects on seed germination. The results demonstrated that Q. liaotungensis seeds possessed high moisture content (96.0%) and germination rate (78.9%) at the time of maturation and dispersal. Regardless of rapid or slow dehydration, germination rate, germination speed, germination index, and vigor index all exhibited a decreasing trend with prolonged dehydration duration and reduced moisture content; after 96 h of dehydration (moisture contents of rapid- and slow-dehydrated seeds were 66.0% and 69.8%, respectively), all seeds lost viability. Seed vigor was significantly positively correlated with moisture content, although mild dehydration could promote germination; rapid-dehydrated seeds demonstrated greater dehydration tolerance than slow-dehydrated seeds. Q. liaotungensis seeds could not tolerate low-temperature storage; germination rate, germination speed, germination index, and vigor index all decreased significantly after 30 d of cold storage at 4 ℃ or 6 h of frozen storage at -4 ℃; after 90 d of cold storage or 48 h of frozen storage, all seeds lost viability.

Full Text

Preamble

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Title: Recalcitrance of *Quercus wutaishanica* Seeds: Sensitivity to Desiccation and Low Temperature
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Abstract

This study investigated the desiccation and low-temperature sensitivity of *Quercus wutaishanica* seeds and their effects on germination using silica gel (rapid desiccation) and a 35 ℃ electric constant-temperature drying oven (slow desiccation), as well as cold (4 ℃) and frozen (-4 ℃) storage. The results showed that *Q. wutaishanica* seeds exhibited high moisture content (96.0%) and germination percentage (78.9%) at shedding. Both rapid and slow desiccation led to decreases in germination percentage, germination rate, germination index, and vigor index with prolonged desiccation time and reduced moisture content. After 96 h of desiccation (with moisture contents of 66.0% and 69.8% for rapid and slow desiccation, respectively), all seeds lost viability. Seed viability showed a significant positive correlation with moisture content, though mild desiccation promoted germination. Rapidly desiccated seeds demonstrated higher desiccation tolerance than slowly desiccated seeds. *Quercus wutaishanica* seeds could not tolerate low-temperature storage, with germination percentage, germination rate, germination index, and vigor index all decreasing significantly after 30 d of cold storage at 4 ℃ or 6 h of frozen storage at -4 ℃. All seeds lost viability after 90 d of cold storage or 48 h of frozen storage.

Keywords: *Quercus wutaishanica*, desiccation tolerance, low temperature storage, seed viability

Introduction

Based on differences in storage behavior, seeds can be classified into two types: orthodox seeds and recalcitrant seeds (Roberts, 1973). Orthodox seeds undergo a distinct dehydration phase during development and can thus be stored long-term at low moisture contents, whereas recalcitrant seeds do not experience maturation drying, maintaining high moisture content and metabolic activity at shedding and consequently exhibiting sensitivity to desiccation (Berjak et al., 2004; Ntuli et al., 2014). Recalcitrant seeds display high, intermediate, and low levels of recalcitrance both within and among species (Wen, 2008; Jayasuriya et al., 2012), and for a given seed lot, desiccation tolerance varies with dehydration rate. Generally, rapid desiccation is considered more favorable for seed survival at lower moisture contents than slow desiccation (Wesley-Smith et al., 2001), as seeds subjected to rapid drying maintain higher viability at equivalent moisture levels. This is attributed to the shorter duration of dehydration stress, which reduces the accumulation of metabolic damage (Walters et al., 2001; Berjak et al., 2004). Conversely, slow desiccation prolongs the period during which water remains in seeds, exacerbating deterioration and causing injury (Waters et al., 2001). For example, when embryonic axes of jackfruit (*Artocarpus heterophyllus*) were dried to a moisture content of approximately 0.37 $g \cdot g^{-1}$, survival rates

were 0% and 100% for slow and rapid desiccation, respectively (Wesley-Smith et al., 2001). Similar dehydration responses have been observed in recalcitrant *Archontophoenix alexandrae* seeds (Shao et al., 2006). In recalcitrant seed biology, moisture content is commonly used as an indicator to evaluate desiccation tolerance (Li et al., 2014), with a critical moisture threshold existing below which viability declines rapidly (Pammenter & Berjak, 2000; He & Song, 2003).

Recalcitrant seeds are not only sensitive to desiccation but also to conventional low-temperature storage conditions due to their high moisture content at maturity (Li & Pritchard, 2009; Walters et al., 2013). Under conditions suitable for orthodox seed storage, recalcitrant seeds generally have short storage lives (Wen, 2008; Berjak & Pammenter, 2013) because no clear boundary exists between the developmental and germination phases, requiring that viability be maintained during storage, which greatly reduces the suitable storage duration and increases the likelihood of spontaneous germination (Xin et al., 2007; Yan et al., 2011). Although recalcitrant seeds from temperate regions cannot tolerate desiccation, they can withstand relatively low temperatures (Wen, 2008). For instance, germination percentage of *Quercus variabilis* seeds showed no significant decline after 100 d of semi-closed storage at 5 ℃, though spontaneous germination was common (Xin et al., 2007). Therefore, developing low-temperature storage techniques for such seeds remains an important practical challenge, particularly for *Quercus* species in temperate regions, whose adaptation to autumn maturation and spring germination means they may face mortality risks from low temperatures during the long winter.

Quercus wutaishanica is a dominant species in the climax deciduous broad-leaved forests of China's warm temperate zone, significantly influencing the appearance, structure, dynamics, and species composition of these communities. Seed-based regeneration plays a crucial role in maintaining genetic diversity and community stability in *Q. wutaishanica*. However, these seeds lack dormancy and can germinate rapidly after shedding. Seed recalcitrance may be widespread in *Quercus* species (Dickie & Pritchard, 2002; Xia et al., 2012). Yan et al. (2011) demonstrated the mild recalcitrance of *Q. wutaishanica* seeds through sand burial and air-dry storage methods, but systematic studies on desiccation and low-temperature tolerance remain lacking. Using *Q. wutaishanica* seeds collected from the Liupan Mountains, this study examined the effects of different desiccation treatments (slow and rapid) and short-term low-temperature storage on seed germination. The results will not only enrich and refine the ecological theory of recalcitrant seeds but also provide practical guidance for developing long-term storage methods and seedling propagation techniques for forestry production.

Materials and Methods

1.1 Seed Collection

Quercus wutaishanica seeds were collected on September 20, 2016, from beneath the canopies of *Q. wutaishanica* trees at Longtan Forest Farm in Liupan Mountain National Nature Reserve (106.9°–106.30° E, 35.15°–35.41° N). Seeds were transported to the laboratory the day after collection, and intact, uniformly sized seeds were selected for use, with a fresh weight of (3.05 ± 0.38) g (n = 100).

1.2 Seed Desiccation and Moisture Content Determination

Rapid desiccation (silica gel treatment): Twenty-seven self-sealing bags (20 cm × 15 cm) were prepared, each containing color-indicating silica gel. Forty selected seeds (seed-to-silica gel mass ratio approximately 1:10) were manually de-coated and placed in each bag in a single layer to ensure full contact with the silica gel. The bags were then placed in a desiccator in the laboratory at approximately 25 ℃. After 1, 2, 4, 8, 12, 24, 48, 72, and 96 h of desiccation, three bags were removed at each time point as three replicates for moisture content and viability determination. Six seeds from each bag were used for moisture content measurement: fresh weight was recorded using an electronic balance, seeds were sliced into approximately 1 mm thick sections with a single-sided blade, and then oven-dried at 103 ℃ for 48 h before re-weighing. Moisture content percentage was calculated on a dry-weight basis. The remaining seeds were used for viability assessment. Both moisture content and viability measurements used newly collected, non-desiccated seeds as controls.

Slow desiccation (constant-temperature oven drying): Twenty-seven petri dishes (120 mm diameter) were prepared. Selected seeds were manually de-coated and placed in a single layer in each dish (40 seeds per dish). The dishes were covered and placed in an electric constant-temperature drying oven at 35 ℃. After 1, 2, 4, 8, 12, 24, 48, 72, and 96 h of desiccation, three dishes were removed at each time point as three replicates for moisture content and viability determination. Moisture content was measured using the same method described above, with the remaining seeds used for viability assessment. Newly collected, non-desiccated seeds served as controls.

1.3 Low-Temperature Storage

Cold storage: Fifteen breathable nylon mesh bags (25 cm × 15 cm) were prepared. Selected seeds were manually de-coated and placed in the bags (30 seeds per bag), which were then stored in a refrigerator at 4 ℃. After 7, 14, 30, 60, and 90 d of storage, three bags were removed at each time point as three replicates for viability determination.

Frozen storage: Eighteen breathable nylon mesh bags of the same size were prepared. After manual de-coating, 30 seeds were placed in each bag and stored

in a freezer at -4 ℃. After 1, 3, 6, 12, 24, and 48 h of storage, three bags were removed at each time point as three replicates for viability determination. Both cold and frozen storage treatments used newly collected, non-stored seeds as controls.

1.4 Seed Germination and Parameter Calculation

Germination was conducted under a 14 h light/10 h dark photoperiod (light intensity approximately 140 $\mathrm{mol \cdot m^{-2} \cdot s^{-1}}$) with temperatures of 25 ℃ during the light period and 15 ℃ during the dark period. Thirty seeds from each desiccation and storage treatment were used for viability assessment. Seeds were sown in petri dishes (12 cm inner diameter) containing approximately 1.5 cm of moist sand (pre-washed with clean water and oven-dried at 103 ℃ for 48 h before use). Seeds were placed flat in the sand and gently pressed to ensure full contact for water absorption. After sowing, dishes were placed in an SPX-330-C intelligent artificial climate chamber (Shanghai Langgan Equipment Co., Ltd.). Germination was recorded every 24 h, with germination defined as radicle emergence of 5 mm (Liu et al., 2005). The number of germinated seeds was recorded, and radicle length was measured. Water was applied as needed to maintain sand moisture, and observations continued until no germination occurred for two consecutive weeks.

Seed vigor parameters evaluated included germination percentage (GP), germination rate (GR), germination index (GI), and vigor index (VI), calculated using the following formulas:

$$\mathrm{GR} = \sum \left(\frac{100 G_i}{n t_i} \right)$$

where n is the number of seeds per treatment, G is the number of seeds germinated on day t ($t = 0, 1, 2, 3, \cdots, \infty$). A higher GR indicates faster germination (Rozema, 1975).

$$\mathrm{GI} = \sum \frac{G_t}{D_t}$$

where G is the number of seeds germinated on day t, and D is the number of days in the germination test.

VI = Germination percentage×[Seedling root length (cm)+Seedling shoot length (cm)] (Boscagli & Sette, 20

(Only radicle length was measured in this study).

1.5 Statistical Analysis

All experimental data were square-root transformed before analysis. Pearson correlation analysis was used to examine the relationship between seed moisture content and germination percentage. One-way ANOVA was employed to analyze differences in moisture content and germination parameters among desiccation stages and between treatments and controls, as well as differences in germination parameters among storage periods and between treatments and controls. All statistical analyses were performed using SPSS 13.0.

Results

2.1 Changes in Moisture Content and Viability During Desiccation

As shown in [Figure 1: see original paper], *Q. wutaishanica* seeds at shedding (non-desiccated) had high moisture content (96.0%). Rapid desiccation significantly reduced moisture content to 89.7% after just 1 h, whereas slow desiccation showed relatively gradual reduction during the first two stages (1 h and 2 h), with a significant decrease to 88.9% only after 4 h. Both desiccation methods showed slightly slower moisture reduction between 4–8 h, after which moisture content decreased rapidly with prolonged desiccation time, with minimal reduction during the final stage (72–96 h).

As shown in [Figure 2: see original paper], both rapid and slow desiccation resulted in decreased seed viability (germination percentage) with reduced moisture content. Pearson correlation analysis revealed significant positive relationships between seed viability and moisture content for both methods (Pearson correlation coefficients of 0.77 and 0.88, respectively, $P < 0.01$). Both methods showed some fluctuation in seed viability during early desiccation stages. However, when seeds reached similar moisture contents (84.1% after 8 h rapid desiccation vs. 83.5% after 12 h slow desiccation), rapidly desiccated seeds showed significantly higher germination percentage (77.8%) than slowly desiccated seeds (58.9%) ($P < 0.05$), with significant differences also observed in germination rate and germination index ($P < 0.05$). After 96 h of desiccation, when moisture contents reached 66.0% and 69.8% for rapid and slow desiccation, respectively, all seeds lost viability.

2.2 Effects of Desiccation on Seed Germination

As shown in [Figure 3: see original paper], non-desiccated *Q. wutaishanica* seeds had a germination percentage of 78.9%. Both rapid and slow desiccation caused an initial fluctuating increase in germination percentage during early stages, reaching maximum values at 4 h (94.4% and 82.2% for rapid and slow desiccation, respectively), with rapid desiccation significantly exceeding the control. With further desiccation, germination percentage decreased continuously, becoming significantly lower than the control after 12 h ($P < 0.05$). After 72 h, germination percentages dropped to 53.3% and 38.9% for rapid and slow

desiccation, respectively, and reached 0% after 96 h.

Desiccation delayed the germination process. Both rapid and slow desiccation caused germination rate to decrease with prolonged desiccation time, with all stages after 8 h showing significantly lower rates than the control ($P < 0.05$), particularly under slow desiccation. After 72 h, germination rates were 4.03 and 1.90 for rapid and slow desiccation, respectively. Notably, rapid desiccation for 4 h slightly increased germination rate, though not significantly different from the control.

Non-desiccated seeds had the highest germination index (3.31), which decreased with desiccation time. Rapid desiccation caused a slight increase after 4 h, but all stages after 8 h were significantly lower than the control ($P < 0.05$). Slow desiccation caused continuous decreases, with all stages after 4 h significantly lower than the control ($P < 0.05$). Minimum values after 72 h were 1.09 and 0.57 for rapid and slow desiccation, respectively.

During rapid desiccation, vigor index showed a fluctuating increase initially, reaching a maximum of 571.03 after 4 h that was significantly greater than the control ($P < 0.05$). It then decreased continuously, reaching a minimum of 283.38 after 72 h, with all stages after 24 h significantly different from the control ($P < 0.05$). During slow desiccation, vigor index increased gradually during the first two stages before 4 h, but without significant differences from the control. All stages after 4 h were significantly lower than the control ($P < 0.05$), decreasing to 211.59 after 72 h.

Note: "n" indicates no significant difference from control seeds; "*" and "**" indicate significant differences from control seeds at $P = 0.05$ and $P = 0.01$, respectively.

2.3.1 Cold Storage

Germination percentage of cold-stored seeds decreased to 71.1% after 7 d (not significantly different from control), dropped significantly to 68.9% after 14 d, then declined sharply to only 5.6% after 60 d and 0% after 90 d. Germination rate decreased from 11.02 in control seeds to 8.49 after 7 d, increased to 10.94 after 14 d, then dropped dramatically to 1.50 and 0.50 after 30 d and 60 d, respectively, all significantly lower than control and 7 d/14 d treatments ($P < 0.05$).

Germination index decreased slightly after 7 d and 14 d (to 2.55 and 3.28, respectively) without significant differences from control, but decreased rapidly to 0.32 and 0.15 after 30 d and 60 d, respectively, both significantly lower than control and other cold storage periods ($P < 0.05$). Vigor index decreased gradually with storage duration, declining from 485.17 in control seeds to 417.38, 380.59, 94.18, and 28.98 after 7, 14, 30, and 60 d, respectively, with significant differences among all storage periods and between treatments and control ($P < 0.05$).

Note: Different lowercase letters indicate significant differences among storage periods. The same notation applies below.

2.3.2 Frozen Storage

Germination percentage of *Q. wutaishanica* seeds decreased significantly after just 1 h of frozen storage (72.2%), then decreased gradually with prolonged storage, reaching only 46.7% after 24 h and 0% after 48 h. Germination rate increased slightly after 1 h (12.27) without significant difference from control, but decreased continuously and significantly with extended storage, with all stages significantly lower than the 1 h treatment ($P < 0.05$). However, except for the 24 h treatment (4.69), other stages were not significantly different from the control.

Germination index increased from 3.31 in control seeds to 3.68 after 1 h, but decreased significantly after 3 h ($P < 0.05$) and continued to decline, reaching a minimum of 1.41 after 24 h that was significantly lower than control and all other frozen storage periods ($P < 0.05$). Vigor index decreased gradually with storage duration, with all periods after 3 h significantly lower than control ($P < 0.05$), reaching a minimum of 253.90 after 24 h that was significantly lower than control and all frozen storage periods except the 3 h treatment ($P < 0.05$).

Discussion

Quercus wutaishanica seeds in the Liupan Mountains typically mature and shed in mid-to-late September, during the late rainy season when the forest floor is moist, allowing immediate germination. These seeds exhibit mild recalcitrance (Yan et al., 2011) and may lose viability if subjected to drought stress. Desiccation sensitivity appears common in *Quercus* species (Dickie & Pritchard, 2002; Xin et al., 2007; Xia et al., 2012). This study confirmed that newly shed *Q. wutaishanica* seeds have high moisture content and germination percentage, with germination percentage, rate, index, and vigor index all decreasing with prolonged desiccation and reduced moisture content under both rapid and slow desiccation conditions. These results verify the typical recalcitrant characteristics of *Q. wutaishanica* seeds (Shao et al., 2006; Xia et al., 2015), which do not undergo pre-maturation dehydration, maintain high moisture content and metabolic activity at shedding, and are therefore sensitive to desiccation—the essence of recalcitrance (Roberts, 1973; He & Song, 2003). Recalcitrant seeds initiate germination before shedding, essentially becoming "seedlings." Rapid germination facilitates prompt utilization of soil moisture, as longer intervals between shedding and germination increase the risk of desiccation damage. Consequently, most recalcitrant seeds germinate quickly after shedding, showing high germination percentages. The desiccation sensitivity and rapid germination characteristics of *Q. wutaishanica* seeds may represent long-term adaptations to their habitat, where seeds shed during the moist late rainy season can germinate immediately. Subsequent winter-spring cold and drought periods can be mitigated by rapid root growth that accesses soil moisture unavailable to

seeds (Berjak & Pammenter, 2013), while also reducing predation and pathogen infection (Jayasuriya et al., 2012). The unique germination process in *Quercus* species rapidly transfers most nutrients from cotyledons to the taproot for storage, ensuring "seedling" survival and growth even if cotyledons are consumed, by relying on taproot reserves the following year (Yan et al., 2012).

Desiccation tolerance in recalcitrant seeds depends not only on the degree of recalcitrance (Xia et al., 2012) but also on desiccation rate. Within certain moisture ranges, faster dehydration rates confer greater tolerance (Walters et al., 2001), allowing recalcitrant seeds or embryos to survive to lower moisture contents while maintaining high viability (Wesley-Smith et al., 2001). Differences in desiccation tolerance under varying rates may relate to the shorter exposure time to intermediate moisture levels during rapid desiccation (Waters et al., 2001; Berjak et al., 2004; Shao et al., 2006), and uneven water distribution in rapidly dried seeds may also enhance tolerance (Tompsett & Pritchard, 1998). However, some studies report no relationship (Pritchard et al., 1995) or even opposite effects, such as in *Baccaurea ramilfora* seeds, which showed greater tolerance during slow desiccation (Lu et al., 2010). In this study, although seed viability was significantly positively correlated with moisture content, rapidly desiccated seeds showed significantly higher germination percentage than slowly desiccated seeds at similar moisture contents after 8 h rapid and 12 h slow desiccation, with significant differences also in germination rate and index. These results suggest that longer water retention times in seeds may increase deterioration damage (Waters et al., 2001), consistent with numerous other reports (Wesley-Smith et al., 2001; Shao et al., 2006). Some researchers propose that rapid desiccation primarily causes mechanical or physical damage (Liang et al., 2002), while the relatively short duration of water-based oxidative accumulation at intermediate moisture levels reduces damage (Pammenter et al., 2000). Slow desiccation may cause metabolic damage through altered metabolism and injury (Walters et al., 2001), though the specific mechanisms require further investigation.

Numerous studies show that mild desiccation can promote germination and increase germination percentages in recalcitrant seeds (Konstantinidou et al., 2008; Lu et al., 2010; Yan et al., 2011). This phenomenon relates to a post-maturation process that may occur at shedding, during which mild desiccation promotes rapid maturation, terminates development-related synthetic events (e.g., storage product synthesis), and initiates germination- and seedling growth-related processes (Song & Fu, 1998), thereby activating the "switch" for germination. In this study, both rapid and slow desiccation caused fluctuating increases in seed vigor during early stages, with germination percentage, rate, index, and vigor index all increasing to maximum values at 4 h, demonstrating that mild desiccation promoted germination. These results support previous findings and may represent an adaptive response where mild desiccation enhances seedling establishment, as rooted seedlings can access soil moisture unavailable to seeds (Berjak & Pammenter, 2013). Consequently, forestry practitioners typically air-dry *Q. wutaishanica* seeds appropriately after collection to promote rapid

germination for direct seeding operations.

Another characteristic of recalcitrant seeds is low-temperature intolerance, which causes viability loss during moist storage (Li & Pritchard, 2009; Walters et al., 2013). Under conditions suitable for orthodox seed storage (low temperature, low moisture, sealed), recalcitrant seed storage life is typically only weeks or months (Berjak & Pammenter, 2013), and may even accelerate death (Wen, 2008). Yan and Cao (2006) suggested that recalcitrant seeds should be stored at temperatures low enough to inhibit or slow germination yet high enough to prevent low-temperature injury, as high moisture content and metabolic activity increase sensitivity to typical low-temperature damage (Li & Pritchard, 2009; Walters et al., 2013). Some highly recalcitrant seeds germinate rapidly under any storage conditions, necessitating storage of already-germinated seeds. Therefore, practical storage of recalcitrant seeds can only delay germination through moderately reduced temperatures (Yan et al., 2011). This study found that although some germination parameters fluctuated slightly during early low-temperature storage, seed viability in both cold and frozen storage decreased with storage duration. Germination percentage, rate, index, and vigor index all decreased substantially after 30 d of cold storage, with only 5.6% of seeds remaining viable after 60 d, and all viability lost after 48 h of frozen storage. These results indicate that although mildly recalcitrant *Q. wutaishanica* seeds can tolerate some low temperature and survive winter under natural conditions (Yan et al., 2011), they can only withstand short-term storage at relatively low temperatures in the laboratory. The lack of a clear boundary between development and germination phases—i.e., the absence of metabolic shutdown mechanisms present in orthodox seeds—leads to widespread spontaneous germination during storage (Devine et al., 2010; Zhou et al., 2013). Additionally, because recalcitrant seed storage requires water-saturated conditions to maintain viability, prolonged storage and increasing spontaneous germination may increase sensitivity to low temperature and desiccation (Yan et al., 2011; Zhou et al., 2013). Other recalcitrant *Quercus* seeds appear more tolerant to low temperature: *Q. variabilis* viability showed no significant decline after 100 d at 5 ℃ (Xin et al., 2007), *Q. ilex* seeds maintained high viability after 11 months at 3 ℃ (Pasquini et al., 2011), and *Q. rubra* seeds could be stored for 3–5 years, albeit with gradually decreasing quality (Bonner & Vozzo, 1987).

Furthermore, seed coats may protect temperate recalcitrant seeds during winter low temperatures. The cold storage temperature in this study (4 ℃) was similar to those used for *Q. variabilis* and *Q. ilex*, yet only 5.6% of *Q. wutaishanica* seeds remained viable after 60 d, suggesting more severe low-temperature damage, possibly because de-coated seeds are more sensitive to low temperature. In nature, besides extensive predation, germination, or fungal infection, some *Q. wutaishanica* seeds can survive through winter under litter protection (personal observation). Zhou et al. (2013) reported that after 12 weeks of outdoor burial at 30 and 50 cm depths, *Q. wutaishanica* seeds maintained over 90% germination despite severe spontaneous germination, indicating that seed

coat protection prevents viability loss during storage. According to Bonner & Vozzo (1987), *Quercus* radicles can rapidly emerge from seeds (spontaneous germination) at 2–5 ℃, similar to the spontaneous germination observed during low-temperature storage in this study. This may reflect long-term adaptation to habitat conditions, as rapid germination at these temperatures transfers most cotyledon nutrients to the taproot (Yan et al., 2012), ensuring seedling survival and growth even if cotyledons are consumed (Yan et al., 2011). Therefore, under natural conditions, *Q. wutaishanica* seeds rely on seed coat protection for enhanced low-temperature tolerance and reduce predation and desiccation risks through spontaneous germination. The local forestry practice that "moderately deep autumn sowing is superior to spring sowing" indirectly confirms this strategy.

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