

## Germination Characteristics and Strategies of Seeds Stored in Canopy and Soil Seed Banks: Postprint

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### Abstract

To elucidate how plant seed banks in the Loess Hilly and Gully region regulate seed germination to enhance individual fitness, seven dominant species with seed banks were selected as study subjects in the research area. Using freshly matured and indoor-stored seeds as controls, we compared the effects of canopy retention (five retention periods) and soil burial (five-year burial period) on seed germination characteristics, and explored seed germination strategies under canopy seed bank and soil seed bank storage. The results demonstrated that after storage in different seed banks, the germination characteristics of the seven plant species exhibited significant interspecific differences. The germination potential of *Rosa xanthina* and *Cotoneaster multiflorus* seeds displayed a canopy-retention-stable type and soil-storage-enhanced type, with soil storage significantly improving the germination rate of *C. multiflorus* seeds. The germination potential of *Lespedeza davurica* and *Sophora davidii* seeds showed a canopy-retention-enhanced type and soil-storage-reduced type, with germination duration exhibiting a canopy-retention-prolonged type; soil seed bank storage could also accelerate the germination rate and shorten the germination duration of *L. davurica*. For *Artemisia giralaui* and *Artemisia gmelinii*, seed germination percentage first increased then decreased with canopy retention time, and first decreased then increased with soil storage time; soil storage could delay their germination, while the germination rate of *A. gmelinii* seeds accelerated after both canopy and soil storage. The germination percentage of *Syringa oblata* seeds first increased then decreased with canopy retention, while soil storage significantly accelerated seed germination initiation and rate. In the Loess Hilly and Gully region, plant seeds stored in canopy or soil seed banks may either increase, accelerate, or advance germination to fully utilize favorable conditions and enhance colonization ability, or decrease, slow, or postpone germination to share the risks of unfavorable conditions. Moreover, the relationship between

germination characteristics after canopy and soil storage in this region reflects division-of-labor and cooperative strategies for environmental adaptation and disturbance response, mainly manifesting as: single-dominant type and complementary type.

## Full Text

### Preamble

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### Seed Germination Characteristics and Strategies of Seeds Stored in Canopy and Soil Seed Banks

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### Abstract

To determine how seed banks regulate seed germination to improve individual fitness in the hilly-gully Loess Plateau region, we selected seven dominant species with prominent seed banks as study subjects. Using freshly matured seeds and laboratory-stored seeds as controls, we compared the effects of canopy persistence (five storage periods) and soil burial (five burial years) on seed germination characteristics, and discussed the germination strategies of seeds stored in canopy and soil seed banks. Our results indicated that germination characteristics of the seven species showed obvious interspecific differences after storage. For *Rosa xanthina* and *Cotoneaster multiflorus*, soil seed bank storage improved seed germination ability while having no effect on canopy seed bank storage, with *C. multiflorus* showing considerable enhancement. For *Lespedeza davurica*, germination ability exhibited a canopy-persistence stable type and soil-storage enhancement type. For *Sophora davidii*, germination ability showed a canopy-persistence enhancement type and soil-storage weakening type. Germination duration displayed a canopy-persistence prolongation type and soil-storage shortening type. Soil seed bank storage also accelerated germination rate and shortened germination duration for *L. davurica*. For *Artemisia giraldii* and *A. gmelinii*, germination percentages initially increased then decreased with canopy storage duration, while soil storage delayed germination. For *A. gmelinii*, germination rates increased after both canopy and soil storage. For *Syringa oblata*, germination percentages initially increased then decreased with canopy storage duration, while soil seed bank storage increased germination rates and promoted germination. In conclusion, seeds from the hilly-gully Loess Plateau either (1) took full advantage of favorable conditions to complete regeneration at the right time quickly by increasing germination percentage, speeding up germination rate, and germinating at high concentration during early storage

stages, or (2) shared the risk of unfavorable conditions by reducing germination percentage, slowing down germination rate, and deferring germination through seed storage in the canopy or soil seed bank. Additionally, the relationship between germination characteristics of canopy storage and soil seed bank storage indicated that plants use the division and cooperation of canopy and soil seed banks to adapt to environments and respond to disturbance, which mainly presented as single-dominant and complementary patterns.

**Keywords:** hilly-gully Loess Plateau; canopy seed bank; soil seed bank; seed germination; seed strategy

## Introduction

Plant seed banks serve as reservoirs for plant regeneration, including soil seed banks and canopy seed banks, with ecological functions of avoiding threats from stress and disturbance to vegetation renewal. The soil seed bank refers to all viable seeds present in soil and upper litter layers, preserving seeds from past and current vegetation as well as external dispersal, reflecting the past, present, and future development potential of communities, and largely determining the pace and direction of plant community development, occupying a very important position in ecosystems [1-3]. Most plants regenerate through soil seed banks [4], which can both protect seeds from various threats and supplement new individuals for disturbed community recovery, holding significant importance in vegetation renewal and restoration [5-8].

In addition to soil seed banks, some plants store seeds in the canopy after maturation, delaying seed release and forming canopy seed banks [9]. Canopy seed banks enable seeds to avoid threats such as predation, yield fluctuations, and unpredictable disturbances, with ecological functions including spreading seed dispersal risk, ensuring continuous seed supply, regulating seed germination timing, sharing seedling establishment risk, and guaranteeing plant habitat occupation [9-10].

Seed germination refers to the process where mature embryos transition to an active state and begin growth after dormancy is broken and suitable external conditions are obtained [11]. As the starting point of plant renewal, germination affects seedling survival, individual fitness, and plant life history expression, playing a key role in population persistence, population dynamics, and community structure [12]. Seed germination is a critical and sensitive stage in plant life history, where seeds utilize their survival strategies to rapidly germinate under suitable environmental conditions, reflecting plant adaptation strategies to environmental stress and holding important significance for successful plant establishment. Seed germination has long attracted attention from scholars worldwide, with research focusing on germination mechanisms and influencing factors, involving molecular biology, morphology, and ecology disciplines. Ecological studies on seed germination have concentrated on external conditions, biological factors, and burial conditions affecting germination, with storage time

shown to alter seed germination processes [13-20]. While research has addressed storage time effects on germination characteristics, the phenomenon of plant seed storage and germination in canopies has received less attention, primarily concentrated in foreign arid desert regions [21-24], with limited domestic reports in the Horqin Sandy Land [25] and Loess Plateau [26-27]. Comprehensive studies on storage effects on germination characteristics are rare, and research combining canopy and soil seed bank storage effects is even scarcer. This study investigates the effects of canopy and soil seed bank storage and their duration on plant seed germination characteristics to explore germination strategies of seeds stored in canopy and soil seed banks in the hilly-gully Loess Plateau region, thereby providing theoretical basis for explaining vegetation processes in this region, clarifying how both seed banks regulate seed germination during vegetation renewal, and guiding vegetation restoration construction and species diversity protection.

## 1. Materials and Methods

### 1.1 Species Selection

Based on previous research and field experience [27-28], we selected seven representative species with both canopy seed banks and soil seed banks in the hilly-gully Loess Plateau region, including the perennial semi-shrubs *Lespedeza davurica*, *Artemisia gmelinii*, and *Artemisia giraldii*, and the shrubs *Sophora davidii*, *Rosa xanthina*, *Syringa oblata*, and *Cotoneaster multiflorus*. The basic characteristics of these species and their seeds are shown in Table 1.

**Table 1** The characteristics of seeds of the study species

Species	Family	Study object	Limitation period of storage
<i>Artemisia gmelinii</i> (Tieganhao)	Compositae	Achene	Soil seed bank [29]
<i>Artemisia giraldii</i> (Jiaohao)	Compositae	Achene	Soil seed bank [29]
<i>Lespedeza davurica</i> (Dawurilespedeza)	Leguminosae	Fruit	Canopy seed bank [27], Soil seed bank [29]
<i>Sophora davidii</i> (Langyaci)	Leguminosae	Fruit	Canopy seed bank [27], Soil seed bank [29]

Species	Family	Study object	Limitation period of storage
<i>Syringa oblata</i> (Zidingxi-ang)	Oleaceae	-	Canopy seed bank [27]
<i>Rosa xanthina</i> (Huancimeimei)	Rosaceae	-	Canopy seed bank [27]
<i>Cotoneaster multiflorus</i> (Shuigouzi)	Rosaceae	-	Canopy seed bank [27]

### 1.2 Collection of Canopy-Persistent Seeds

To investigate the effects of canopy storage on seed germination, we established five stable communities in Songjiagou and Zhifanggou watersheds in the Yanhe River basin that included all study species. Collection times were selected at five different periods: the first collection period was based on seed maturation completion dates for all surveyed species (A1), followed by different canopy storage periods at A2 (2012), A3 (2012), A4 (2012), and A5 (2012). For each species, no fewer than 30 individual plants were sampled, with seeds collected from the same plant following the principle of uniform spatial distribution. Collected seeds were placed in paper bags and brought back to the laboratory, where well-developed and intact seeds were selected. For seeds wrapped in pulp, manual pulp removal was performed, and the screened seeds were mixed uniformly.

### 1.3 Soil Seed Bank Storage Experiment

At seed maturity, test seeds were prepared according to the above collection and processing methods. Seeds were placed in mesh bags of appropriate size and pore diameter [30], with 100 well-developed and intact seeds randomly selected for each species. Each species had 35 replicate bags, with burial depths set at 0.1 m based on the maximum distribution depth of soil seed bank density [28]. At the end of October, seeds were buried in the Dunshan experimental field of the Ansai County Soil and Water Conservation Research Station, Chinese Academy of Sciences. Five 1 m × 10 m sample belts were selected in the experimental field, with seven 1 m × 1.5 m plots established in each belt. In each plot, 35 burial pits were dug in a 5 × 7 arrangement, each measuring 0.2 m × 0.2 m × 0.1 m. Mesh bags were placed in the pits with seeds spread evenly to avoid clustering and increased decay. Samples were collected annually after burial, with three replicate mesh bags randomly collected for each species and brought back to the laboratory for air-drying and processing to count intact seeds.

#### 1.4 Determination of Seed Germination Characteristics

Germination characteristics were determined through indoor germination experiments. For canopy seed bank seeds, three replicates were set for each species, with 50 seeds per replicate for small seeds and 30 seeds per replicate for large seeds. For soil seed bank seeds, three replicates were set for each species, with the germination base number varying by seed size and collected sample size. Since intact seed numbers varied after soil burial, the number of intact seeds after burial was used as the germination base number (Table 2).

**Table 2** The initial germination seeds after different buried years of the 7 study species

Species	Freshly matured	1 year	2 years	3 years	4 years	5 years
<i>A. gmelinii</i>	48.2±11.6	38.2±11.4	44.2±2.1	85.8±1.8	5.2±1.5	99.4±0.6
<i>A. giraldii</i>	97.6±1.6	2.8±0.4	18.0±3.0	59.3±1.8	80.7±3.0	92.0±12.2
<i>L. davurica</i>	88.7±8.4	18.3±17.3	31.0±0	73.5±0.5	65.8±19.4	69.0±3.0
<i>S. davidii</i>	67.8±2.6	1.0±0	22.5±21.5	58.5±9.5	80.8±3.1	44.3±24.0
<i>S. oblata</i>	21.7±10.6	13.0±12.0	71.0±1.0	71.3±3.0	30.2±5.1	9.0±2.9
<i>R. xanthina</i>	-	-	-	-	-	-
<i>C. multiflorus</i>	-	-	-	-	-	-

Germination experiments were conducted in an artificial climate incubator. Based on multi-year average meteorological observation data from the study area, culture conditions were set at 25°C for 13 h during the day (light intensity 8800 lx) and 16°C for 11 h at night. Petri dishes (9 cm diameter) with double-layer filter paper were used as culture beds, sterilized with hot water. Seed germination was defined as embryo breakthrough of the seed coat. Germinated seeds were counted daily starting from seed placement until no germination occurred for three consecutive days [31]. Germination characteristics were represented by the following indices:

1. **Germination percentage (%)** = (Total germinated seeds / Tested seeds) × 100%
2. **Germination lag time (d)**: Duration from seed placement to germination initiation
3. **Germination duration (d)**: Duration from first seed germination to germination completion

4. **T** : Time required for germinated seeds to reach 50% of total germination, representing germination rate

## 1.5 Data Analysis

Differences in germination percentage, germination lag time, and germination duration under different storage conditions were analyzed using one-way ANOVA and least significant difference (LSD) tests ( $\alpha = 0.05$ ) with SPSS 20.0 software. SigmaPlot 13.0 was used for data statistics and analysis.

## 2. Results

### 2.1 Effects of Different Seed Bank Storage on Germination Percentage

Canopy seed bank and soil seed bank storage had different effects on plant seed germination percentage. After storage in different seed banks, the seven plant species showed obvious interspecific differences in germination ability. *Rosa xanthina* and *Cotoneaster multiflorus* seeds did not germinate at all when freshly matured or after winter storage at room temperature, but germinated at extremely low rates after different canopy persistence periods, showing a persistence-stable type. Soil seed bank storage promoted their germination ability, showing a burial-enhancement type. *Lespedeza davurica* and *Sophora davidii* seeds had certain germination ability when freshly matured, with germination percentages increasing to varying degrees after winter storage and canopy persistence. However, after soil seed bank storage, their germination percentages were generally lower than those of freshly matured and room-temperature-stored seeds. Except for *L. davurica* seeds, which showed increased germination after 1 year of soil burial, the overall pattern was canopy-persistence enhancement type and soil-burial weakening type. *Artemisia giraldii* and *A. gmelinii* seeds showed increased germination percentages after room-temperature storage and canopy persistence compared to freshly matured seeds, indicating these species require certain after-ripening for germination. As canopy persistence time increased, germination percentages decreased to varying degrees. After soil burial, *A. giraldii* and *A. gmelinii* seeds showed a trend of first decreasing then increasing germination percentages, indicating short-term burial weakening type and long-term burial enhancement type. *Syringa oblata* seeds showed significantly reduced germination after soil burial ( $P < 0.05$ ) but exhibited an initial increase followed by decrease with canopy persistence.

[Figure 1: see original paper] **Fig. 1** The germination percentages of seeds stored in different conditions during different times. Germinate directly just after mature (Fresh); IS: Germinate after stored at room temperature from mature to next spring; A1-A5: Germinate after stored on canopy for periods of 1 month, 3.5 months, 5 months, 6 months and 7 months respectively; S1-S5: Germinate after stored in soil for periods of 1, 2, 3, 4 and 5 years respectively. Different small letters mean significant difference at 0.05 level.

## 2.2 Effects of Different Seed Bank Storage on Germination Rate

The seven plant species showed varied responses in germination rate to different seed bank storage conditions. Canopy persistence and soil storage had relatively small effects on *Artemisia giraldii* germination rate. *Artemisia gmelinii* seeds showed shortened  $T$  after different canopy persistence periods, indicating improved later-stage germination rate. Both canopy persistence and soil storage increased germination rates for *A. gmelinii*. Canopy seed bank and soil seed bank storage both affected *Sophora davidii* germination rate, with faster rates completing germination shortly after placement. *Lespedeza davurica*  $T$  initially shortened then lengthened with canopy persistence time, with small changes in early persistence stages but considerable prolongation with extended persistence. Except for *L. davurica* seeds after 1 year of soil burial, which showed shortened  $T$ , all other burial years showed shortened  $T$ . *Syringa oblata* seeds showed large fluctuations in  $T$  after canopy persistence. *Cotoneaster multiflorus* and *Rosa xanthina* seeds did not germinate before burial. After burial, *C. multiflorus* generally showed accelerated germination rate with increasing burial years, showing typical burial-acceleration type, while *R. xanthina* showed unstable, fluctuating germination rates after burial. For most study species, canopy persistence and soil burial had consistent effects on germination rate, with increased rates in early germination stages and corresponding increases in later stages. Some species showed opposite response trends, such as *A. gmelinii* seeds showing initial prolongation then shortening of  $T$  after canopy persistence, and *A. giraldii* and *S. davidii* seeds showing initial shortening then prolongation after soil burial.

[Figure 2: see original paper] **Fig. 2** The germination rates of seeds stored in different conditions during different times.

## 2.3 Effects of Different Seed Bank Storage on Germination Pattern

Canopy seed bank and soil seed bank storage affected germination patterns of the seven species differently, manifested in germination lag time and germination duration. For germination lag time, *Artemisia giraldii* and *A. gmelinii* seeds had 0-day lag time when freshly matured. Canopy seed bank persistence affected their germination lag time differently: *A. giraldii* showed a trend of prolonged germination lag time, while *A. gmelinii* showed relatively earlier germination initiation with non-significant changes. After soil seed bank storage, these two species generally showed relatively earlier germination initiation. Except for *A. gmelinii* seeds after 4 years of burial, which had only 0.8-day lag time, all other conditions showed delayed germination initiation. Moreover, *A. gmelinii* seeds showed progressively delayed germination initiation with increasing burial years, showing typical burial-delay type. *Syringa oblata* seeds showed overall shortening of germination lag time after both canopy persistence and soil storage. *Lespedeza davurica* and *Sophora davidii* seeds showed fluctuating changes in germination lag time with canopy persistence. The analysis revealed that most seeds were in deep dormancy state with difficulty initiating germina-

tion, resulting in long lag times. Some individual seeds that had just broken dormancy during canopy persistence showed short lag times under sufficient moisture conditions. After soil storage, *L. davurica* seeds continued to show fluctuating lag time, while *S. davidii* seeds showed initial shortening then prolongation. *Rosa xanthina* and *Cotoneaster multiflorus* seeds only germinated after soil storage, with large variation in lag time.

For germination duration, *Artemisia giraldii* seeds showed shortened germination duration with extended canopy persistence time, while soil seed bank storage showed fluctuating effects on germination duration, likely related to the fluctuating fate of small seeds in soil. Except for canopy persistence at 5 months, both canopy persistence and soil storage significantly shortened germination duration for *A. gmelinii* ( $P < 0.05$ ). *Lespedeza davurica* seeds showed increasing germination duration with extended persistence time, while soil storage had relatively small effects. *Syringa oblata* seeds showed overall shortening after soil storage. *Sophora davidii* seeds maintained long germination duration after canopy persistence but showed shortened duration after soil storage. *Rosa xanthina* seeds showed an overall trend of initial prolongation then shortening with increasing soil burial years, while *Cotoneaster multiflorus* seeds maintained long germination duration after 1 year of burial, then shortened significantly in subsequent years, always remaining relatively short. *A. gmelinii* seeds had longer germination duration when freshly matured.

[Figure 3: see original paper] **Fig. 3** The days of germination and before germination of seeds stored in different conditions during different times.

### 3. Discussion

#### 3.1 Germination Strategies and Ecological Significance of Canopy Seed Bank Storage

In arid and semi-arid regions, canopy seed banks can indirectly affect seed germination by regulating seed dispersal timing to adapt to drought environments [21–25, 32]. The study area belongs to a semi-arid monsoon region with distinct rainy seasons, where rainfall accounts for 47.3% of annual precipitation, mostly as heavy storms, accompanied by extreme drought events after rainfall, creating drought stress. Except for *Cotoneaster multiflorus*, seeds in canopy seed banks of other study species can persist until the next year, effectively spreading the risk of extreme drought events. Canopy seed banks delay seed dispersal and germination to the rainy season, ensuring successful regeneration through persistent seed supply.

During canopy persistence, seeds experience external light, temperature, and moisture cycles that alter dormancy status and affect germination characteristics, with different species showing different coping strategies. Typical psammophyte seeds in canopy storage have rapid germination characteristics, improving plant recruitment and establishment success as an adaptation to shifting sand and seasonal drought [25]. The extremely dormant *Lespedeza davurica* seeds in

this study showed increased germination percentage after 5 months of canopy persistence, adapting to the rainy season's adequate water supply for germination and seedling survival, demonstrating the advantageous strategy of canopy storage promoting germination. *Cotoneaster multiflorus* and *Rosa xanthina* seeds did not germinate during different canopy persistence periods, indicating their canopy seed bank strategy only regulates seed dispersal without functioning in germination regulation.

Different species regulate germination rate and pattern to exert the advantageous ecological functions of seeds after canopy storage. Seeds germinated relatively earlier after canopy persistence, with *Sophora davidii* seeds showing 5–6 days earlier germination in the next June compared to freshly matured seeds. This characteristic adapts to the uneven precipitation distribution in the study area, where surface soil moisture remains dry for long periods, making rapid germination initiation important for seizing favorable rainfall events to complete germination and renewal quickly [27], consistent with previous studies on ecological functions of canopy seed banks in arid regions [9, 22].

Changes in germination characteristics after canopy seed bank storage also reflect responses to external disturbances. Canopy-stored seed germination shows certain responses to sand burial disturbance [15]. In the hilly-gully Loess Plateau, water erosion causes slope soil erosion and deposition, providing more favorable germination conditions for canopy seeds through inflorescences or reproductive branches. For example, *Artemisia gmelinii* seeds on the canopy showed shortened germination lag time with extended persistence time, especially when arriving at suitable destinations through water erosion action during the rainy season, seizing favorable conditions to initiate germination quickly, reflecting the response of canopy seed bank storage to water erosion in the study area.

### 3.2 Germination Strategies and Ecological Significance of Soil Seed Bank Storage

Soil seed bank storage provides direct seed source guarantee for vegetation renewal, offering seed reserves along temporal sequences. It not only has ecological functions for adapting to environmental stress and disturbance threats in unstable environments but also reduces intra- and inter-specific competition in stable environments [1]. Soil seed banks provide different microhabitats for stored seeds. Habitat heterogeneity is not only a determinant of soil seed bank distribution patterns but also directly changes plant seed germination characteristics through non-biological factors such as soil mechanical structure and disturbance type, affecting the spatiotemporal distribution of soil seed banks and vegetation development [33–34]. Soil seed banks enable seeds to increase reproductive fitness by regulating dormancy and germination [35].

Soil seed bank storage effects on germination characteristics first manifest in germination ability. Plant seeds show obvious interspecific differences in germi-

nation ability after soil storage, especially for hard seeds. Hard seed dormancy benefits plants by regulating spatiotemporal distribution of germination, with germination percentages changing during storage depending mainly on temperature and humidity [36]. *Rosa xanthina* and *Cotoneaster multiflorus* seeds did not germinate at all when freshly matured or after winter storage at room temperature due to hard seededness. Hard seeds cannot imbibe and germinate because of poor seed coat permeability and mechanical restriction on embryo growth [36]. However, soil seed bank storage enhanced their germination ability because the storage process facilitates contact between hard woody shells and soil microorganisms. Seeds experience imbibition, cell wall resistance decreases, seed coat restriction weakens [36], promoting water entry. When seeds experience hot summers in soil, higher temperatures facilitate microbial decomposition of seed coats [37], giving them the ability to germinate under suitable conditions. This indicates soil seed bank storage is a prerequisite for germination and renewal of these two species, thus holding important ecological significance.

Hard-seeded *Lespedeza davurica* and *Sophora davidii* seeds showed weakened germination after soil seed bank storage, with enhanced dormancy. This mainly results from differences in seed coat cell layers, arrangement, types and content of impermeable substances, and mechanical strength among different plants [35, 37–38]. Legume seed coats are very tough, with the outer cuticle layer mainly composed of hydrophobic chemicals such as hemicellulose and pectin, and inner layers widely developed with palisade cells and osteosclerids forming a strong, dense protective layer [39–40]. Legume hilum often functions to allow water loss but prevent water entry, closing rapidly in humid air [37, 40]. These two germination types reflect two seed germination strategies for adapting to environmental stress and disturbance in this region: burial-enhancement type can seize suitable conditions to complete germination and renewal, while burial-weakening type can avoid threats from unfavorable conditions and provide seed source guarantee after disturbance.

*Lespedeza davurica* and *Sophora davidii* seeds showed weaker germination and stronger dormancy in soil storage than under other conditions. Moreover, seeds buried for 1 year in plots without vegetation cover showed more germination than those buried in other plots, possibly because less light penetration in soil [41] makes hard seed coat breaking more restrictive, though the mechanism requires further study. While light promotes germination of some plant seeds, it inhibits others [42]. *Artemisia giraldii* and *A. gmelinii* seeds showed reduced germination percentages after burial, indicating short-term soil seed bank storage inhibits their germination, helping them avoid risks from unfavorable conditions during early disturbance stages. This reflects that soil seed bank storage beyond certain time can promote germination, helping stored seeds seize favorable rainfall events to complete germination quickly, which is advantageous for coping with frequent and intense rainfall events in arid and semi-arid regions [25].

Soil storage also regulates germination patterns to adapt to environments. Burial can delay germination of *Artemisia giraldii* and *A. gmelinii* to avoid

threats from brief favorable conditions followed by unfavorable conditions. By shortening germination duration of *A. gmelinii*, burial improves success of rapid germination completion under brief suitable conditions. Moreover, *Rosa xanthina* and *Cotoneaster multiflorus* seeds adopt strategies of slow germination after short-term burial and rapid germination after long-term burial to cope with environmental stress. After soil storage, germination percentages of most plant species increased, with germination rates accelerating, helping stored seeds seize favorable precipitation events to complete germination quickly.

The germination characteristics of seeds after canopy and soil seed bank storage show certain relationships, reflecting division and cooperation functions for adapting to environments and responding to disturbances. Single-dominant type: *Rosa xanthina* and *Cotoneaster multiflorus* seeds showed canopy-persistence stable type, reflecting a strategy of using soil storage to promote germination for coping with long-term uncertain disturbances. Complementary type: *Lespedeza davurica* and *Sophora davidii* seeds showed canopy-persistence enhancement type and soil-storage weakening type, reflecting a short-long term complementary strategy where canopy persistence adapts to short-term growing season renewal while soil storage adapts to long-term seed source needs after uncertain disturbances.

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

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