# Seed Dormancy and Germination Characteristics of Heteromorphic Fruits of *Lycium ruthenicum* in Heterogeneous Habitats (Postprint)

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**Date:** 2023-08-25T00:00:00+00:00

## Abstract

Lycium ruthenicum is a national second-class protected plant with both medicinal and edible properties in the arid regions of northwestern China. In natural populations of southern Xinjiang, two types of individuals bearing flat-shaped and spherical fruits occur, with their proportions differing among populations at various altitudes. To understand the germination characteristics of seeds from heteromorphic fruits of this species in populations at different altitudes and their responses to desert environments of different climate types, comparative controlled laboratory experiments were conducted on seed set rate and seed quality, dormancy, germination characteristics, and responses to drought stress in populations at different altitudes, aiming to reveal the responses of heteromorphic fruits of this species to desert environments at different altitudes in southern Xinjiang. The results showed that the seed set rate of flat-shaped fruits of L. ruthenicum was higher than that of spherical fruits; the seed set rate of heteromorphic fruits gradually decreased with increasing population altitude, while seed quality gradually increased with altitude. The water absorption rate of seeds from low-altitude populations was higher than that of high-altitude populations, and the water absorption rate of seeds from flat-shaped fruits was higher than that of seeds from spherical fruits. High temperature (20–30 °C), low-concentration (0.1 mmol・$L^{-1}$) gibberellin, and complete darkness were the main factors breaking dormancy. Seeds from spherical fruits showed higher responsiveness to high-concentration 30% PEG drought stress than seeds from flat-shaped fruits; the drought resistance of fruits from low-altitude populations was higher than that of high-altitude populations.

## Full Text

# Seed Dormancy and Germination Characteristics of Heteromorphic Fruits of *Lycium ruthenicum* in Heterogeneous Habitats

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## Abstract

*Lycium ruthenicum* is a national second-class protected plant used for both food and medicine in the arid regions of Northwest China. In natural populations of southern Xinjiang, two types of individuals produce flat and spherical fruits, with their proportions varying among populations at different elevations. To understand the germination characteristics of heteromorphic fruit seeds across different elevational populations and their responses to desert environments with varying climate types, we conducted comparative controlled laboratory experiments on seed set and quality, dormancy, germination traits, and drought stress responses across different elevational populations, aiming to reveal how heteromorphic fruits of this species respond to desert environments at different elevations in southern Xinjiang. The results showed that flat fruits of *L. ruthenicum* had higher seed set than spherical fruits; the seed set of heteromorphic fruits gradually decreased with increasing elevation, while seed quality gradually increased with elevation. Seeds from low-elevation populations had higher water absorption rates than those from high-elevation populations, and seeds from flat fruits had higher water absorption rates than seeds from spherical fruits. High temperature ( ), low-concentration gibberellin (0.1 mmol $\cdot$ $L^{-1}$), and complete darkness were the main factors breaking dormancy. Seeds from spherical fruits showed greater drought resistance to high-concentration 30% PEG, and this resistance was higher in low-elevation populations than in high-elevation populations.

**Keywords:** *Lycium ruthenicum*; heteromorphic fruit; seed dormancy; bet-hedging; adaptive strategy; elevation

## Introduction

During their long evolutionary history, angiosperms have evolved survival capabilities and adaptive mechanisms to cope with various environments, including deserts and alpine regions. Due to heterogeneity in natural resources and other biotic and abiotic environmental conditions, individual species exhibit different adaptive characteristics in morphological structure, physiological function, and reproductive traits. In particular, polymorphism or heteromorphism in fruit and seed morphology (shape, size, mass) and ecological behaviors (dormancy, germination, and seedling growth) ensures reproductive success and offspring fitness. Related studies suggest that fruit or seed heteromorphism represents an optimal adaptation strategy for seed plants to survive in heterogeneous environments.

*Lycium ruthenicum* belongs to the family Solanaceae and genus *Lycium*, and is a national second-class protected plant resource used for both food and medicine. In China, it grows in various ecosystems at elevations of 1100–3200 m in Northwest China, including Ningxia, Qinghai, Inner Mongolia, Gansu, and Xinjiang. It is most widely distributed in desert and alpine environments in southern Xinjiang (southwest of the Taklamakan Desert). In the natural distribution area of southern Xinjiang, this species produces both homostylous and distylous flowers, with homostylous flowers that have higher selfing rates producing flat berries, while distylous flowers with higher outcrossing rates produce spherical berries. Both fruit types are black-purple with reniform seeds. This study used the two fruit types from three different elevational populations as research material (Fig. 1 [Figure 1: see original paper]) for controlled laboratory experiments.

The study sites were located in plain and alpine desert environments at different elevations in the southwestern Taklamakan Desert region (Table 1 ). The low-elevation Artux desert environment belongs to the warm temperate desert climate type, while the Aktao and Taxkorgan alpine desert environments belong to the cold temperate climate type. Significant differences existed among natural populations in elevation, rainfall, average annual temperature, sunshine duration, and flowering time of the species (Table 1 ). Specifically, average annual temperature gradually decreased from low to high elevations, while rainfall increased from low-elevation plain deserts to high-elevation plateau deserts.

## Methods

### 1.1 Study Materials and Sites

*Lycium ruthenicum* produces two fruit types from distylous and homostylous flowers with significant differences in shape, size, and weight. Significant differences in fruit mass, shape, and size existed among populations at different elevations, which may be related to temperature affecting fruit development, resource allocation by plants, and pollination mode.

### 1.2.1 Natural Seed Set and Water Absorption Characteristics

**(1) Natural seed set:** To determine the natural seed set of heteromorphic fruits in different natural populations, 30 fruits of each type were randomly selected at the fruit ripening stage in each population, and the number of intact seeds per fruit was counted. Natural seed set = (number of intact seeds per fruit)/200 × 100%. Thirty fruits of each type were randomly selected, and seed length and width were measured using a portable SE2000 electronic vernier caliper (Guilin Digit Electronic Co., Ltd., Guilin, China; precision 0.02 mm). Simultaneously, ten-seed weight was measured using an FA1004 electronic balance (Huafeng Electronic Instrument Factory, Ningbo, China; precision 0.0001 g), with three replicates per measurement.

**(2) Seed water absorption characteristics:** To assess differences in water absorption characteristics of seeds from heteromorphic fruits among different natural populations, 30 intact and plump seeds from each fruit type were selected and divided equally into three groups (three replicates). The mass of each group was measured using an electronic balance. Each group of seeds was placed in a petri dish (9 cm diameter) with two layers of filter paper, and an appropriate amount of distilled water was added. Seeds were incubated in complete darkness at 2–5 °C, and the mass of each group was measured every 2 h until seed mass no longer increased. Finally, seed water absorption rate (Wr) was calculated using the method of Baskin et al.: Wr = (Wf –Wi)/Wi × 100%, where Wi and Wf represent seed mass before and after water absorption, respectively. Differences in water absorption rates were compared between the two fruit types across different natural populations.

### 1.2.2 Effects of Light and Temperature on Seed Germination

To determine the effects of light and temperature on seed germination of the two heteromorphic fruit types, freshly matured fruits were collected from different natural populations of *L. ruthenicum* and brought back to the laboratory. Fruits and seeds were separated, and intact, plump seeds were placed in petri dishes with two layers of filter paper (50 seeds per dish, three replicates). Seeds were then incubated in temperature-light incubators under three different temperature regimes (2–5 °C, 10–20 °C, and 20–30 °C) and three different light conditions (normal incubator light and complete darkness, with petri dishes wrapped in opaque black bags) for 30 days. To maintain consistent moisture levels across petri dishes under different temperature and light treatments, 0.5 mL of distilled water was added to each dish daily, and germination was recorded daily. At the end of the experiment, the viability of non-germinated seeds was tested using 1% 2,3,5-triphenyltetrazolium chloride (TTC) solution, where viable seeds would stain red or pink.

### 1.2.3 Effects of Gibberellin Treatment on Seed Germination

To determine the effects of gibberellin ($GA_3$) concentration on seed germination of heteromorphic fruits from different natural populations of this species, intact and plump seeds were placed in petri dishes with two layers of filter paper (50 seeds per dish, three replicates). $GA_3$ solutions at concentrations of 0, 0.1, 1, and 10 $mmol \cdot L^{-1}$ were added to the dishes, which were then sealed with parafilm and wrapped in opaque black bags. Seeds were incubated for 30 days under three temperature regimes (2–5 °C, 10–20 °C, and 20–30 °C) in complete darkness. To maintain stable solution concentration and moisture levels in the petri dish microenvironment, 0.5 mL of the corresponding $GA_3$ solution was added to each dish every five days under complete darkness, and germination percentage was recorded.

### 1.2.4 Effects of Drought Stress (PEG) on Seed Germination

To assess the effects of drought stress on seed germination of heteromorphic fruits from different natural populations of this species, seeds were placed in petri dishes with two layers of filter paper (50 seeds per dish, three replicates). Polyethylene glycol (PEG 6000) solutions at concentrations of 0, 10%, 20%, and 30% were added to the dishes. Seeds were incubated for 30 days under three temperature regimes (2–5 °C, 10–20 °C, and 20–30 °C) in complete darkness. To maintain stable solution concentration and moisture levels in the petri dish microenvironment, 0.5 mL of the corresponding PEG solution was added to each dish every five days under complete darkness, and germination percentage was recorded.

### 1.3 Data Processing

All data in this study were analyzed using SPSS 22.0 statistical software. Prior to analysis, all data were tested for normal distribution and homogeneity of variance. For data following a normal distribution, a Generalized Linear Model (GLM) with an identity function was used to compare seed set, water absorption characteristics, seed size, and ten-seed weight of heteromorphic fruits. A binomial distribution with Logistic link function was used to analyze and compare seed germination percentages. Tukey' s HSD test from one-way ANOVA was used to examine significant differences among treatments ($\alpha = 0.05$). Statistical data are presented as mean ± SE, and figures were created using Sigma Plot 14.0 software.

## Results

### 2.1 Natural Seed Set and Water Absorption Characteristics

The natural seed set of the two heteromorphic fruit types of *L. ruthenicum* was significantly affected by fruit type ($F = 57.40$, $P < 0.001$) and population ($F = 97.17$, $P < 0.001$), but not by their interaction ($F = 4.62$, $P = 0.10$). Flat fruits had higher seed set than spherical fruits, and the natural seed set of both fruit types gradually decreased from low-elevation plain desert (Artux) populations to high-elevation alpine desert (Taxkorgan) populations (Fig. 2 [Figure 2: see original paper]). Seed size and weight differed between the two fruit types. Ten-seed weight of heteromorphic fruits was affected by population, fruit type, and their interaction. Specifically, ten-seed weight of spherical fruits gradually increased from low- to high-elevation populations, whereas ten-seed weight of flat fruits gradually decreased from low- to high-elevation populations (Fig. 2 [Figure 2: see original paper]). Seed length of heteromorphic fruits was affected by population ($F = 23.21$, $P < 0.001$) and population × fruit interaction (F =

15.27, $P < 0.001$), but not by fruit type ($F = 0.41$, $P = 0.62$). Seed length of both fruit types gradually increased from low to high elevations (Fig. 2 [Figure 2: see original paper]), whereas seed width was not affected by population ($F = 1.94$, $P = 0.38$), fruit type ($F = 1.17$, $P = 0.28$), or their interaction ($F = 2.28$, $P = 0.69$) (Fig. 2 [Figure 2: see original paper]).

Seeds from both fruit types rapidly absorbed water within 24 h, followed by slow water absorption over the subsequent 72 h (Fig. 3 [Figure 3: see original paper]). Seed water absorption rates gradually decreased from high- to low-elevation populations. Flat fruit seeds showed greater water absorption increments than spherical fruit seeds, and the water absorption rates of both fruit types showed varying degrees of positive correlation with population rainfall. These results indicate that average annual rainfall is the primary factor influencing seed water absorption characteristics.

### 2.2 Effects of Light and Temperature on Seed Germination

Seed germination percentages of flat and spherical fruits were affected by population, temperature, fruit type, population × temperature, population × fruit type, population × light, temperature × fruit type, temperature × light, fruit type × light, temperature × fruit type × population, temperature × population × light, fruit type × light, and interactions among these factors. However, light, fruit type × light, temperature × fruit type × light, and population × light interactions had no significant effects on seed germination (Fig. 4 [Figure 4: see original paper], Table 2 ).

Seed germination percentages of both fruit types under dark conditions at different temperatures were higher than those under light conditions (Fig. 4 [Figure 4: see original paper]). Flat fruit seeds showed lower germination percentages than spherical fruit seeds across different temperatures and light conditions (light and dark) (Fig. 4 [Figure 4: see original paper]). Germination percentages of both fruit types at low temperature (2–5 °C) were lower than those at 10–20 °C and 20–30 °C, with germination percentages gradually increasing from low to high temperatures under different light conditions (Fig. 4 [Figure 4: see original paper]). These results indicate that high temperature and dark conditions are the main factors breaking seed dormancy in both fruit types of this species. Seeds from both fruit types at different temperatures and light intensities in high-elevation populations showed lower germination percentages than other populations, indicating obvious intermediate physiological dormancy. In contrast, non-deep physiological dormancy existed in Aktao and Artux populations, where dark conditions at 20–30 °C promoted seed germination percentages of both fruit types in low-elevation populations (Fig. 4 [Figure 4: see original paper]). These findings suggest that the trade-off relationship between seed dormancy and germination percentage in different elevational populations may be a factor affecting population structural stability.

### 2.3 Effects of Gibberellin Treatment on Seed Germination

Under dark conditions, temperature, fruit type, population, and $GA_3$ concentration had significant effects on seed germination (Table 2 ). Additionally, interactions between temperature × fruit type, temperature × population, temperature × $GA_3$, fruit type × population × $GA_3$, population × fruit type × $GA_3$, and temperature × population × $GA_3$ significantly affected seed germination (Table 2 ).

The effects of $GA_3$ concentration on seed germination were stronger than those on spherical fruits under different temperature conditions. $GA_3$ at 0.1 $mmol \cdot L^{-1}$ promoted seed germination percentages in Artux and Aktao populations, whereas high-concentration $GA_3$ (10 $mmol \cdot L^{-1}$) inhibited seed germination. Low concentration (0.1 $mmol \cdot L^{-1}$) could break seed dormancy in heteromorphic fruits of *L. ruthenicum*, with 0.1 $mmol \cdot L^{-1}$ being the optimal concentration for breaking seed dormancy (Fig. 5 [Figure 5: see original paper]). Germination percentages of both fruit types in the high-elevation Taxkorgan population increased under high-temperature (20–30 °C) dark conditions (Fig. 5 [Figure 5: see original paper]). Seed germination percentages of both fruit types in the Artux population were lower than those in Aktao and Taxkorgan populations. These results indicate that $GA_3$ had the most pronounced effects on seeds from both fruit types in the high-elevation Taxkorgan population, with negative effects on germination of flat fruit seeds. Specifically, under high-temperature conditions, $GA_3$ had stronger effects on germination percentages of flat fruit seeds than on spherical fruit seeds.

### 2.4 Effects of Drought Stress (PEG) on Seed Germination

Under dark conditions, PEG concentration, fruit type, population, and temperature had significant effects on seed germination (Table 2 ). Additionally, interactions between PEG concentration × fruit type, PEG concentration × population, PEG concentration × temperature, fruit type × population, fruit type × temperature, and population × temperature significantly affected seed germination (Table 2 ).

Polyethylene glycol (PEG) at different concentrations had negative effects on seed germination in populations at different elevations, with the most pronounced effects on the high-elevation (Taxkorgan) population. The effects on spherical fruits were lower than those on flat fruits. Under different temperature conditions, the effects of PEG concentration on seed germination were stronger than those on spherical fruits. These results indicate that higher drought stress inhibited seed germination to some extent in different populations and fruit types.

## Discussion

### 3.1 Differences in Seed Quality of Heteromorphic Fruits in Heterogeneous Environments

Differences among heteromorphic fruits (seeds) are primarily manifested in morphological structures such as fruit/seed shape and size. Variation in fruit (seed) size and number is a central issue in plant fitness studies and a key factor affecting population dynamics, interspecific interactions, and community succession. For example, *Leontodon saxatilis* in the Asteraceae family produces two types of fruits (dark brown and light brown), while in the distylous plant *Primula nivalis* across different elevational populations, short-styled flowers produce heavier seeds than long-styled flowers. In this study, *L. ruthenicum* produced spherical and flat fruits with significant differences in shape, size, and weight from distylous and homostylous flowers. Significant differences in fruit mass, shape, and size existed among populations at different elevations, which may be related to temperature affecting fruit development, resource allocation by plants, and pollination mode. Differences in fruit and seed mass can be explained through the "stress tolerance" and "energy limitation" hypotheses. The former suggests a positive correlation between seed weight and population elevation, with larger seeds having greater advantages for seedling establishment and survival at high elevations. The latter suggests a negative correlation between seed weight and population elevation because low temperatures and short growing seasons at high elevations can affect photosynthetic rates and energy required for seed development. For instance, in *Pedicularis*, the number of seeds per fruit positively correlates with elevation, while in the distylous plant *Primula atrodentata*, seed set, 100-seed weight, and germination percentage of short-styled selfing morphs first decreased then increased with elevation. To adapt to different survival environments, plant seeds exhibit flexible adaptive and reproductive strategies. For example, germination of *Caragana korshinskii* seeds under low temperature and soil moisture conditions in early spring may compensate for the inhibitory effects of high temperature and soil moisture on seed germination in summer and autumn. *Erodium oxyrhynchum* autumn-germinating plants produce numerous small seeds to increase genetic diversity and environmental adaptability of offspring, while spring-germinating plants produce fewer, larger, and more stable seeds to enhance seedling survival under salt stress. Differences in morphological (size, color, shape, and mass) structures and physiological (dispersal, dormancy, germination, and seedling growth) behavioral characteristics of heteromorphic fruit seeds are considered important features for understanding species' seasonal variation and spatial distribution patterns. To adapt to heterogeneous environmental conditions such as temperature, light, water, and nutrients, heteromorphic fruits exhibit a mixed reproductive strategy of "bet-hedging."

### 3.2 Germination and Dormancy of Heteromorphic Fruit Seeds

Researchers suggest that seed germination and dormancy are affected by temperature and climate gradient changes. In this study, seeds from freshly harvested fruits of both types of *L. ruthenicum* showed germination and dormancy characteristics adapted to heterogeneous habitats under different temperature and light conditions. Both fruit types germinated only under high-temperature (20–30 °C) dark conditions, but not under low-temperature conditions (Fig. 4 [Figure 4: see original paper]). High temperature and darkness were the main factors affecting differences in seed germination percentages between the two fruit types. Seed germination percentages of both heteromorphic fruit types were higher under dark conditions than under light conditions. High germination percentages under summer high-temperature conditions represent an adaptation to environmental stress in high-elevation grassland populations of *L. ruthenicum*. Additionally, significant differences existed in seed germination percentages treated with different $GA_3$ concentrations ($P < 0.05$). $GA_3$ at 0.1 $mmol \cdot L^{-1}$ increased germination percentages of seeds from both fruit types in the Taxkorgan population under high-temperature conditions (Fig. 5 [Figure 5: see original paper]). Seeds from low-elevation plain desert populations showed higher germination percentages at 20–30 °C than seeds from high-elevation alpine desert populations.

### 3.3 Response of Heteromorphic Fruits to Drought Stress in Heterogeneous Habitats

Temperature, light, and water are factors affecting seed germination, among which water plays an important role in breaking seed dormancy and promoting germination. Plants in arid desert environments have evolved drought-resistant germination strategies to avoid population extinction during long-term adaptation to drought. As a desert plant, *L. ruthenicum* already possesses drought stress adaptation capabilities. In this study, indoor PEG-simulated drought stress experiments showed that seeds from both fruit types in different elevational populations had higher germination percentages under high-temperature dark conditions than under low-temperature conditions, and germination inhibition increased with increasing PEG concentration. These results indicate that higher drought stress inhibited seed germination to some extent in different populations and fruit types. Therefore, in the three desert environments with uneven precipitation distribution and timing (Table 1 ), seeds from heteromorphic fruits of this species have evolved different response strategies to water requirements. In low-elevation populations, when fruits matured in late July, seeds from both fruit types attempted seedling establishment through rapid germination under high-temperature conditions. Under these conditions, drought stress had no obvious effect on spherical fruits, whereas germination percentages of flat fruit seeds were inhibited by drought stress. When the rainy season arrived in August, massive germination produced more seedlings.

## Conclusion

This study investigated the effects of different elevational gradients on seed dormancy and germination characteristics of heteromorphic fruits of *L. ruthenicum*, leading to the following conclusions: (1) Seed set of heteromorphic fruits gradually decreased from low-elevation plain desert (Artux) populations to high-elevation alpine desert (Taxkorgan) populations, with flat fruits having higher seed set than spherical fruits. Ten-seed weight of spherical fruits gradually increased from low- to high-elevation populations, whereas the opposite pattern was observed for flat fruits. (2) Seed germination percentages under dark conditions at different temperatures were higher than those under light conditions. Spherical fruit seeds showed higher germination percentages than flat fruit seeds, and germination percentages of both fruit types gradually increased from low to high temperatures under different light conditions. (3) Gibberellin ($GA_3$) had certain promoting effects on seed germination. Specifically, at 0.1 mmol · $L^{-1}$ concentration, seed germination percentages of both fruit types increased under high-temperature conditions in the high-elevation Taxkorgan population. Seeds from low-elevation plain desert populations showed higher germination percentages at 20–30 °C than seeds from high-elevation alpine desert populations. Spherical fruit seeds demonstrated stronger drought resistance to PEG than flat fruit seeds. During long-term survival in three natural populations with distinct rainfall differences, this species has evolved different drought resistance strategies, with seed germination percentages decreasing as water potential declined.

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