

Physiological and Biochemical Characteristics of Spring- and Autumn-Germinated *Erodium oxyrhynchum* Plants and Their Progeny Seeds (Postprint)

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Abstract

Using the early spring ephemeral plant *Erodium oxyrhynchum*, which exhibits a spring/autumn germination phenomenon in the Gurbantünggüt Desert, as experimental material, this study investigated the phenotypic plasticity and differences in reproductive strategies between spring- and autumn-germinated individuals by analyzing the biological, physiological, and biochemical characteristics of the plants and their offspring seeds. The results showed: (1) During winter, autumn-germinated *E. oxyrhynchum* plants resisted stress damage through the accumulation of proline and soluble sugars; (2) In stressful environments, spring-germinated plants primarily relied on superoxide dismutase (SOD) and catalase (CAT) to scavenge the toxicity produced by reactive oxygen species (ROS), whereas autumn-germinated plants mainly depended on peroxidase (POD) and CAT for detoxification; (3) Comprehensive resistance evaluation indicated that autumn-germinated plants exhibited greater resistance than spring-germinated plants; (4) The seed number per autumn-germinated plant exceeded 60, with a 100-seed weight of $0.323 \pm 0.0026g$; *theseednumberperspring – germinatedplantwasapproximately20, witha100 – seedweightof* $0.376 \pm 0.0014g$; (5) Correlation analysis of various seed indices revealed that under high and low temperature stresses, the content of four internal substances in seeds showed a significant positive correlation with the antioxidant enzyme system. Additionally, the brassinosteroid (BR) content in spring-germinated plant seeds exhibited a significant negative correlation with the three antioxidant enzymes, whereas the BR content in autumn-germinated plant seeds showed a significant positive correlation with antioxidant enzymes; (6) Seed trait network analysis demonstrated that continuous high and low temperature stresses affected the network complexity of *E. oxyrhynchum* seeds, with spring-germinated plant

seeds exhibiting higher network complexity than autumn-germinated plant seeds; under stressful conditions, the correlations among various physiological and biochemical indices were stronger in spring-germinated plant seeds. Overall, autumn-germinated *E. oxyrhinchum* plants demonstrated stronger resistance and tended to produce numerous, small seeds, thereby conferring greater genetic diversity to offspring and enhancing species adaptability to environmental conditions; spring-germinated plants, with weaker resistance, produced fewer but larger and more stable seeds, which facilitated seedling survival under stressful environments. This flexible adaptive strategy reflects the phenotypic plasticity of *E. oxyrhinchum* and the divergent survival and reproductive strategies between spring- and autumn-germinated plants.

Full Text

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**Physiological and Biochemical Characteristics of Spring/Autumn-
Germinated Plants and Progeny Seeds of *Erodium oxyrrhynchum***

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Abstract

Using *Erodium oxyrrhynchum*, a dominant early-spring ephemeral plant in the Gurbantunggut Desert that exhibits both spring and autumn germination, this study investigated the phenotypic plasticity and reproductive strategy differences between spring- and autumn-germinated individuals through analysis of biological, physiological, and biochemical characteristics of parent plants and progeny seeds. The results demonstrated that: (1) Autumn-germinated plants accumulated proline and soluble sugars during winter to resist stress damage. (2) In stressful environments, spring-germinated plants primarily relied on superoxide dismutase (SOD) and catalase (CAT) to scavenge reactive oxygen species (ROS) toxicity, whereas autumn-germinated plants mainly depended on peroxidase (POD) and CAT for detoxification. (3) Comprehensive resistance evaluation revealed that autumn-germinated plants exhibited greater resistance than spring-germinated plants. (4) Autumn-germinated plants produced over 60 seeds per plant with a 100-seed weight of 0.323 ± 0.0026 g, while spring-germinated plants produced approximately 20 seeds per plant with a 100-seed

weight of 0.376 ± 0.0014 g. (5) Correlation analysis of seed indices showed that under high- and low-temperature stress, seed inclusion content was significantly positively correlated with the antioxidant enzyme system. Additionally, brassinosteroid (BR) content in spring-germinated plant seeds was significantly negatively correlated with three antioxidant enzymes, while BR content in autumn-germinated plant seeds was significantly positively correlated with the antioxidant enzyme system. (6) Seed trait network analysis indicated that continuous high- and low-temperature stress affected seed network complexity, with spring-germinated plant seeds showing higher network complexity than autumn-germinated plant seeds. Under stress conditions, physiological and biochemical indices of spring-germinated plant seeds showed stronger correlations.

Overall, autumn-germinated *E. oxyrrhynchum* plants demonstrated stronger resistance and tended to produce numerous, smaller seeds, thereby conferring greater genetic diversity to progeny and enhancing species adaptability to environmental conditions. Spring-germinated plants, with weaker resistance, produced fewer but larger and more stable seeds that facilitated seedling survival under stressful conditions. This flexible adaptive strategy reflects the phenotypic plasticity of *E. oxyrrhynchum* and the divergent survival and reproductive strategies between spring- and autumn-germinated individuals.

Keywords: *Erodium oxyrrhynchum*; asynchronous germination; physiological and biochemical characteristics; resistance; phenotypic plasticity; reproductive strategy

Introduction

The Gurbantunggut Desert, located deep within the Eurasian continent, is China's largest fixed and semi-fixed desert with a typical temperate continental arid climate characterized by harsh natural conditions vulnerable to anthropogenic disturbance and extreme climatic events. Compared with other desert regions, this area harbors relatively rich plant resources, including a unique plant functional group—ephemeral and pseudo-ephemeral plants—that constitutes an important component of China's desert ecosystem. Ephemeral plants are herbaceous species that rapidly complete their life cycles within short timeframes, primarily inhabiting arid environments where they can quickly emerge and develop using early-spring precipitation and snowmelt, completing their life cycle before the onset of hot, dry summer conditions. Typically germinating in early spring, these plants can also respond rapidly to adequate moisture availability within specific time windows, exhibiting seed heterochrony germination—a crucial trait representing phenotypic plasticity.

Phenotypic plasticity refers to the capacity of the same genotype to express different phenotypic traits in response to varying environmental conditions, manifested in morphology, physiology, and other aspects that can be transmitted across generations. Transgenerational plasticity, also termed maternal environmental effects, enables parent plants to transmit environmental information

and changes to offspring, inducing plastic phenotypic changes in progeny. Such maternal effects can influence seed size, germination, physiology, and other phenotypic characteristics, with phenotypic plasticity directly reflecting plant adaptability to different environments. Investigating phenotypic plasticity and adaptive traits is crucial for validating plant ecological adaptation and evolutionary theories, and desert ephemeral plants capable of asynchronous germination represent ideal materials for such research.

During growth, plants may experience various types and degrees of environmental stress, with adaptation capacity reflected through physiological and biochemical indices. Osmotic regulation represents a key mechanism for resisting adversity, where cells may lose water under stress conditions, prompting plants to actively accumulate various osmotic regulators to reduce cellular osmotic potential, thereby maintaining turgor pressure and influencing other physiological and biochemical activities. Stressful environments also cause excessive accumulation of reactive oxygen species (ROS) such as hydrogen peroxide (H_2O_2) during normal metabolic processes. ROS are highly toxic and can damage intracellular proteins, carbohydrates, and genetic materials when accumulated to certain levels, while also inducing membrane lipid peroxidation to produce malondialdehyde (MDA), inhibiting normal plant growth. Consequently, plants possess antioxidant defense mechanisms to continuously scavenge excess ROS.

Seeds represent the primary means of plant progeny continuation, with carbohydrates constituting their main nutritional components, while lipids protect cell membranes from damage and proteins participate in cellular structure. Plant hormones including abscisic acid (ABA), gibberellin (GA), and auxin (IAA) play major regulatory roles in seed dormancy, germination, and seedling growth, whereas brassinosteroids (BR) not only control plant temperature and photomorphogenesis, enhance stress resistance, and promote cell elongation, but also facilitate seed germination. Therefore, seed inclusions and hormonal components regulate seed germination and seedling growth. Current research on ephemeral plant seeds has primarily focused on morphological biology and germination characteristics, with limited reports on seed physiological and biochemical properties and their variations under different environmental conditions.

Erodium oxycarrhynchum is a common early-spring ephemeral plant in the Gurbantunggut Desert with seed heterochrony germination characteristics, belonging to the Geraniaceae family and *Erodium* genus. This annual herbaceous species inhabits deserts and arid Gobi regions, distributed only in northern Xinjiang and the Kashgar area of China. *E. oxycarrhynchum* plays a prominent role in windbreak and sand fixation, exhibits high sensitivity to environmental changes, and possesses important ecological and biological functions. Spring-germinated plants emerge in March-April annually, while autumn-germinated plants emerge in October-November, overwintering at different growth stages and resuming growth in March-April of the following year to complete their life cycle by early summer. Previous studies have found that autumn-germinated *E. oxycarrhynchum* exhibited higher leaf numbers, individual crown width, biomass,

100-seed weight, and root mycorrhizal infection rates than spring-germinated plants at all growth stages, with significant differences observed. However, scientific questions regarding whether physiological and biochemical differences exist between autumn- and spring-germinated plants and their seeds, and how reproductive strategies differ, remain unclear. Therefore, to better understand the physiological responses of desert ephemeral plants to environmental conditions, this study used *E. oxvrrhynchum* as material to analyze morphological characteristics and physiological and biochemical stress responses of parent plants and seeds, thereby elucidating the relationship between phenotypic plasticity and environmental variation, describing survival and reproductive strategies under adverse conditions, enriching understanding of stress resistance mechanisms in ephemeral plants, and accumulating theoretical foundations for studying desert vegetation responses and adaptations to adversity.

1.1 Study Area

The study area was located at the southern edge of the Gurbantunggut Desert in the Junggar Basin hinterland (44°26' N, 87°54' E), characterized by a typical temperate continental arid climate with hot summers and long, cold winters. The region has an annual mean temperature of 6.6°C, accumulated temperature of 3000–3500°C, annual precipitation of 70–150 mm, and annual potential evaporation of 2000 mm.

1.2 Methods

1.2.1 Plant Leaf Collection and Physiological-Biochemical Index Detection In 2019–2020, leaves of *E. oxvrrhynchum* were collected at different growth stages in the Gurbantunggut Desert, immediately treated with liquid nitrogen, and transported to the laboratory for physiological and biochemical analysis. Growth stage classifications were: for spring-germinated plants—cotyledon stage (late March, early spring snowfall), initial leaf-expansion stage (early April), leaf-expansion stage (mid-April), flowering stage (early May), fruiting stage (mid-May), and pre-withering stage (late May); for autumn-germinated plants—cotyledon stage (mid-October, pre-snowfall), initial leaf-expansion stage (early November), leaf-expansion stage (post-snowfall early November), leaf-expansion stage (early March of following year), flowering stage (early April), fruiting stage (mid-April), and pre-withering stage (late April, early spring snowfall). Measured indices included osmotic regulator contents (soluble protein, proline, and soluble sugar) and antioxidant enzyme activities (SOD, POD, CAT), along with H₂O₂ and MDA contents.

Osmotic regulator content was determined using test kits: proline via acidic ninhydrin colorimetry, soluble sugar via anthrone colorimetry, and soluble protein via Coomassie brilliant blue G-250 method. Antioxidant enzyme activities were measured using test kits: SOD activity via WST-8 method, POD activity via guaiacol method, and CAT activity via visible colorimetry. H₂O₂ and

MDA contents were determined using sulfuric acid titanium colorimetry and thiobarbituric acid methods, respectively.

1.2.2 Comprehensive Resistance Evaluation of Plants Fuzzy membership functions were used to comprehensively evaluate resistance of spring- and autumn-germinated *E. oxycorymbosum* plants:

$$R(X_{ij}) = \frac{X_{ij} - X_{j\min}}{X_{j\max} - X_{j\min}}$$

where X_{ij} represents the measured value of a physiological index for a test plant, $X_{j\max}$ is the maximum value of that index, and $X_{j\min}$ is the minimum value. Membership values for each physiological index of spring- and autumn-germinated plants were calculated at different growth stages, averaged across stages, and then summed and averaged across all indices to obtain overall resistance membership values for comparison.

1.2.3 Seed Collection and Physiological-Biochemical Index Determination In autumn, autumn-germinated *E. oxycorymbosum* plants were marked in the field experimental plot, with spring-germinated plants marked the following spring. Seeds were collected in May and June. For each plant, seed number, reproductive biomass, and seed biomass were measured. Collected seeds were subjected to stress treatments and analyzed for germination rate, 100-seed weight, inclusions, antioxidant enzyme system, and hormones.

Seed treatments: Based on surface temperature data from 2018–2020 at a meteorological station near the field site (Table 1), newly collected spring- and autumn-germinated plant seeds were stored under three treatments simulating field seed burial environments, with germination rate, 100-seed weight, inclusions, and physiological indices measured.

Treatment 1: 29.5°C for 10 h → 50°C for 2 h → 29.5°C for 10 h (total darkness, 5 cycles)

Treatment 2: 16.2°C for 10 h → 1.8°C for 2 h → 16.2°C for 10 h (total darkness, 5 cycles)

Treatment 3: 10 h at -2.7°C → 2 h at -5°C → 10 h at -2.7°C (total darkness, 5 cycles)

Reproductive plant measurements: During mid-to-late May, reproductive-stage spring- and autumn-germinated plants were collected. Seed number was counted in the field, plants were cleaned, reproductive parts separated, placed in envelopes by germination type, returned to the laboratory, killed at 105°C for 30 minutes, and weighed.

Germination rate determination: Seeds from spring- and autumn-germinated plants under three treatments and a control group were placed in natural germination (control) and physical scarification groups in 9 cm

diameter petri dishes lined with two layers of filter paper, with 50 seeds per dish and three replicates per treatment. Dishes were placed in an incubator at optimal germination temperature (25°C/10°C, 12 h light/12 h dark) with daily distilled water addition. Germination counts (radicle emergence as criterion) were recorded daily for 15 days.

100-seed weight determination: Seeds from spring- and autumn-germinated plants under three treatments and control were cleaned and weighed using a Sartorius BS124S electronic balance (0.0001 g precision), with five replicates of 100 seeds each.

Seed inclusion determination: Seeds under three treatments and control were analyzed for soluble sugar, crude fat, soluble protein, and starch contents. Crude fat was determined via Soxhlet extraction, and starch via anthrone colorimetry.

Antioxidant enzyme system determination: Seeds under three treatments and control were analyzed for SOD, POD, and CAT activities, along with MDA and H₂O₂ contents.

Hormone determination: Seeds under three treatments and control were analyzed for ABA, GA, IAA, and BR contents using high-performance liquid chromatography.

1.3 Data Processing

Data were analyzed using IBM SPSS Statistics and graphed using Origin 2021. One-way ANOVA was used to analyze 各项指标 of spring- and autumn-germinated plants and seeds. Fuzzy membership functions evaluated plant resistance. Correlations between temperature and various indices of spring- and autumn-germinated seeds were analyzed and visualized via correlation heatmaps. Seed trait networks were constructed using RStudio with psych and igraph packages.

2 Results

2.1 Physiological and Biochemical Indices of Spring/Autumn-Germinated Plants

Overall, autumn-germinated plants at the leaf-expansion stage (pre-snowfall) showed significantly different physiological and biochemical indices compared with other growth stages, whereas spring-germinated plants exhibited relatively minor variations across stages. Before snowfall, proline and soluble sugar contents in autumn-germinated plants increased significantly, while soluble protein content decreased sharply. After spring snowmelt, autumn-germinated plants maintained relatively stable levels. Spring-germinated plants showed relatively stable osmotic regulator contents throughout development (Figure 1). Before winter, antioxidant enzyme activities in autumn-germinated plant leaves

increased significantly with decreasing temperatures, while MDA and H_2O_2 contents rose sharply (Figure 2). After the following spring, autumn-germinated plants maintained high antioxidant enzyme activities with low MDA and H_2O_2 levels (Figure 3). Spring-germinated plants maintained stable SOD activity from cotyledon to pre-withering stages, POD activity showed a decreasing-then-increasing trend, and CAT activity increased with plant development, while MDA and H_2O_2 remained consistently low (Figure 3).

2.2 Membership Function Values and Comprehensive Resistance Evaluation

Fuzzy membership function analysis of soluble sugar, soluble protein, proline, SOD, POD, CAT, MDA, and H_2O_2 yielded overall membership values (Table 2). Spring-germinated plants showed slightly higher soluble protein and SOD membership values than autumn-germinated plants, while autumn-germinated plants exhibited higher membership values for all other indices. Based on comprehensive evaluation of osmotic regulators, antioxidant enzymes, MDA, and H_2O_2 , autumn-germinated plants demonstrated higher overall resistance than spring-germinated plants.

2.3 Reproductive Biomass, Seed Number, and 100-Seed Weight per Plant

Autumn-germinated *E. oxyrrhynchum* plants produced significantly higher reproductive biomass and seed numbers per plant than spring-germinated plants (Figure 4). Autumn-germinated plants yielded over 60 seeds per plant, while spring-germinated plants produced approximately 20 seeds per plant. Although reproductive biomass differed significantly between germination types, with autumn-germinated plants showing substantially higher values, reproductive allocation was similar at 52.7% for spring- and 48.7% for autumn-germinated plants. Spring-germinated plant seeds exhibited significantly greater 100-seed weight than autumn-germinated plant seeds (Figure 4).

2.4 Germination Rate and 100-Seed Weight of Spring/Autumn-Germinated Seeds Under Different Treatments

Continuous high- and low-temperature stress significantly improved natural germination rates of *E. oxyrrhynchum* seeds. In control groups, spring-germinated seeds showed significantly higher natural germination rates than autumn-germinated seeds, but after treatment, no significant differences existed between germination types (Figure 5). Following physical scarification to break physical dormancy, both spring- and autumn-germinated seeds achieved over 90% germination across all treatments, with no significant treatment effects on 100-seed weight.

2.5 Physiological and Biochemical Indices of Spring/Autumn-Germinated Seeds

Hormone analysis revealed that seeds of both germination types were sensitive to temperature treatments, with significant differences in hormone contents between spring- and autumn-germinated seeds (Figure 6). Inclusion analysis showed that high- and low-temperature stress significantly increased seed inclusion contents. Crude fat content showed continuous increase under high-then-low temperature treatment, while other indices increased initially then plateaued. Autumn-germinated seeds exhibited significantly higher starch content but lower soluble sugar content than spring-germinated seeds (Figure 7). High- and low-temperature stress stimulated production of three antioxidant enzymes in seeds, with MDA and H_2O_2 contents decreasing as enzyme activities increased. Spring-germinated seeds showed significantly higher SOD and POD activities than autumn-germinated seeds (Figure 8).

2.6 Correlation Analysis Among Seed Indices

Correlation heatmaps visualized relationships among physiological and biochemical indices of spring- and autumn-germinated seeds under continuous temperature stress (Figure 9). Spring- and autumn-germinated seeds showed correlations among hormone contents, inclusion contents, and antioxidant enzyme physiological indices under stress. Inclusion contents were significantly positively correlated with antioxidant enzyme systems (correlation coefficients: 0.70576-0.93555, $P < 0.01$). BR content in autumn-germinated seeds was significantly positively correlated with antioxidant enzyme activities (correlation coefficient: 0.8396, $P < 0.01$), while BR content in spring-germinated seeds was significantly negatively correlated with antioxidant enzymes (correlation coefficients: -0.8396 to -0.94857, $P < 0.01$).

2.7 Seed Trait Network Analysis of Spring/Autumn-Germinated Plants

Based on measurements and correlation analyses, seed trait networks were constructed for spring- and autumn-germinated seeds (Figure 10), with traits as nodes and inter-trait relationships as edges to visualize complex networks. Continuous high- and low-temperature stress affected seed network complexity, with low-temperature stress reducing inter-index correlations. Spring-germinated seed networks showed higher complexity than autumn-germinated seeds, reflecting stronger correlations among physiological and biochemical indices under stress.

3 Discussion

Plant phenotypic plasticity is intimately linked to environmental conditions. Plant trait formation results from combined effects of multiple environmental factors. In this study, heterogeneous habitats of spring- and autumn-germinated

E. oxycorymbum resulted from differences in germination timing, with seeds showing different physiological responses to environmental variation, reflecting specialized survival strategies for the Gurbantungut Desert.

Plant stress resistance is reflected through physiological and biochemical indices. Osmotic regulators proline and soluble sugar are typically positively correlated with resistance—higher contents reduce cellular water loss and increase survival under adverse conditions. Studies on cruciferous ephemeral plants show that with increasing drought stress, proline and soluble sugar contents increase substantially while soluble protein changes little, indicating that plants primarily accumulate soluble sugars and proline to maintain cellular turgor. In this study, autumn-germinated plants showed significantly increased proline and soluble sugar contents before winter snowfall when temperatures dropped sharply, while soluble protein decreased dramatically. After spring snowmelt, proline and soluble sugar contents in both germination types were low and stable, while autumn-germinated plant soluble protein increased significantly compared with pre-snowfall levels. Thus, autumn-germinated plants resisted winter stress through proline and soluble sugar accumulation, while spring-germinated plants with low proline and soluble sugar contents experienced less environmental stress.

Plants produce substantial ROS under stress, which can damage membranes and macromolecules. Enzymatic protection systems including SOD, POD, and CAT scavenge ROS cooperatively, maintaining ROS at low levels to avoid cellular damage. In this study, autumn-germinated plants showed sharp POD activity increases before snowfall, indicating enhanced membrane lipid peroxidation with intensifying stress. After spring resumption, autumn-germinated plants maintained high POD and CAT activities with low MDA and H₂O₂ levels. Spring-germinated plants maintained stable SOD activity throughout development, with higher SOD activity than autumn-germinated plants, while autumn-germinated plants showed higher POD activity. This suggests that under stress, spring-germinated plants primarily used SOD and CAT for detoxification, while autumn-germinated plants relied mainly on POD and CAT.

Plant stress resistance is complex, influenced by multiple factors and interactions among indices. When individual indices cannot adequately reflect stress tolerance, fuzzy membership function analysis provides a comprehensive evaluation method. This study used fuzzy membership functions to evaluate resistance across complete life cycles, revealing greater resistance in autumn-germinated plants, likely due to their longer life history and more complex stress experiences.

Seed size is a key, relatively stable life history trait influenced by genetics and environment, representing adaptation to local conditions. In this study, spring-germinated plants produced fewer, larger seeds while autumn-germinated plants produced numerous, smaller seeds, possibly related to individual plant size. Research shows that seed yield in monocarpic plants correlates positively with individual size, and previous studies confirmed that autumn-germinated

E. oxyrrhynchum individuals had substantially greater biomass and 2-10 times higher seed numbers than spring-germinated plants. Larger temperature fluctuations in arid regions benefit germination of physically dormant seeds, and this study's temperature treatments significantly improved germination of physically dormant *E. oxyrrhynchum* seeds, indicating that variable temperatures promote dormancy break.

Seed physiological studies revealed correlations among indices, with spring- and autumn-germinated seeds showing different responses. Under continuous temperature stress, soluble sugar inclusions were significantly positively correlated with antioxidant enzymes, likely reflecting rapid metabolic adjustments to scavenge ROS and maintain membrane integrity. BR content showed opposite correlations: negative in spring-germinated seeds but positive in autumn-germinated seeds. Research indicates that within certain ranges, increasing BR enhances plant stress resistance, but high BR concentrations can cause excessive ROS accumulation. In this study, spring-germinated seeds had high initial BR concentrations that decreased sharply after stress, while autumn-germinated seeds showed low initial BR that increased further after stress, suggesting different BR-mediated regulatory strategies.

Large seeds generally exhibit greater stress resistance than small seeds, but resistance requires comprehensive assessment. This study used Pearson correlation analysis to construct correlation matrices, then visualized relationships as seed trait networks using R. The higher network complexity in spring-germinated seeds under stress suggests greater homeostatic capacity, potentially benefiting seedling establishment under adverse conditions.

4 Conclusion

This study on *Erodium oxyrrhynchum*, a common species in the Gurbantungut Desert with spring and autumn germination, analyzed parent plant and progeny seed biological, physiological, and biochemical characteristics, yielding the following conclusions:

- 1) **Parent plants:** Overwintering autumn-germinated plants experienced more complex stress conditioning, stimulating greater production of antioxidant enzymes (POD, CAT) and osmotic regulators (proline, soluble sugar). These physiological and biochemical indices played important roles in resisting environmental stress, particularly low-temperature stress, enhancing ROS scavenging and antioxidant capacity, inhibiting MDA production, and maintaining osmotic balance, thereby demonstrating stronger physiological resistance. Spring-germinated plants developing under more favorable conditions experienced milder stress, with lower overall antioxidant enzyme and osmotic regulator contents and weaker physiological resistance.
- 2) **Progeny seeds:** Spring-germinated plants tended to produce fewer, larger seeds, while autumn-germinated plants produced numerous, smaller

seeds. Continuous high- and low-temperature stress facilitated dormancy break and promoted germination. Simulated seasonal temperature treatments significantly affected seed physiological and biochemical indices. Seed trait network analysis based on 14 physiological indices revealed that spring-germinated seeds had higher network complexity and overall stability than autumn-germinated seeds.

- 3) **Ecological implications:** Autumn-germinated plants with broader ecological amplitude tended to produce numerous, small seeds, conferring greater genetic diversity to progeny, though small seeds contained less energy and had poorer stability, potentially relying on other mechanisms such as inherited “stress memory” for seedling establishment. Spring-germinated plants, with weaker stress resistance, produced fewer, larger seeds containing more energy that facilitated seedling establishment under stress. This flexible adaptive strategy demonstrates the phenotypic plasticity of *E. oxycorymbosum* and divergent survival and reproductive strategies between germination types.

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

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