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Regional Variation in Seed Germination and Dormancy of *Juniperus foetidissima* Willd. in Azerbaijan

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Seeds of Juniperus foetidissima are vulnerable to germination depending on the environmental conditions such as temperature, elevation, soil conditions, etc. The inhibition of germination may also be species specific and result from dormancy mechanism. Seeds from four ecological zones of the Republic of Azerbaijan were subjected to warm-cold stratification in order to improve their germination rate. The these areas comprised the Greater Caucasus on the northern slopes, the Lesser Caucasus, Talysh Mountains with the Lankaran–Lerik area, and the Nakhchivan Autonomous Republic. The collected seeds were placed under warm and moist conditions at the temperature of 20-22°C for 4 weeks and then under cold-moist conditions at 4-5°C for 10-12 weeks. The results showed that seed source and stratification treatments had significant effects on the germination rate. Among the various regions, seeds from the mountainous regions above 1,000 m had the best germination percentages under normal conditions, particularly those from the Lesser Caucasus and Nakhchivan Autonomous Republic. These seed lots, after a combined warm–cold stratification treatment, showed significantly improved germination, with a clear dependence on dormancy-breaking treatments. Plants from high mountain areas usually have a higher germination rate since they experience a natural long stratification period. Lower germinating rates are observed with seeds from lower elevations (Talysh region (Lankaran–Lerik)) even after stratification. This difference is mostly attributable to genetic adaptation to the local climate, which is not as cold as in other parts of the world where it is more important.
Keywords: *Juniperus foetidissima*, seed germination, cold-moist stratification, regional variation.

INTRODUCTION

J. foetidissima is classified as Least Concern (LC) on the IUCN (International Union for Conservation of Nature) Red List (Proutsos et al., 2021). It is a tree reaching 5–6 m in height, sometimes up to 16 m, with a pyramidal to oval crown, or a shrub approximately 1.5 m tall. The branches are relatively dense, predominantly monopodial, and arch upward in a curved manner. The bark is gray in adult plants and brownish-red in young individuals.

The stems of *J. foetidissima* are thick and quadrangular, with bark that exfoliates easily. The leaves are scale-like, dark green, arranged in whorls of three at the juvenile stage, elongated rhomboid to lanceolate-rhomboid, 2–10 mm long and about 2 mm wide, and loosely appressed to the shoots. When crushed, the leaves emit a strong unpleasant odor (Farhat et al., 2023).

J. foetidissima may possess both reproductive systems on the same plant or separately (monoecious or dioecious). Cones are berry-like cones, 10 mm in diameter, blackish-reddish, usually with a glaucous coating. Seeds 1–2, rarely 3, ovoid, light brown. The propagation of plant is by seeds and vegetative cuttings. Cones are matured in the second year, from October to December. Seed dispersal is by birds, and pollination is by wind (anemophilous) and occurs in April–May. Ecologically, *J. foetidissima* is considered a mesophyte, meaning that it is adapted to habitats with moderate moisture availability and does not typically occur under extremely dry or waterlogged conditions. It also thrives on calcareous, stony, rocky, or clayey grey-brown soils (International Union for the Protection of New Varieties of Plants, 2007;

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Korenkova, 2023).

J. foetidissima possesses a well-developed root system, with roots distributed both in the upper soil horizons and in deeper layers. According to Rzaeva (2021), the average lifespan of *J. foetidissima* may reach 300–400 years. The species is relatively undemanding in terms of soil conditions and can tolerate moderate salinity, which increases its potential value for planting in environmentally constrained areas (Proutsos et al., 2021; Dillard, 2025).

Although J. foetidissima has ecological value for stabilizing soils and maintaining vegetation cover in mountainous and degraded habitats, its natural regeneration remains limited by low and delayed seed germination (Caser et al., 2025). This limitation is especially important in regions where restoration and ex situ propagation depend on reliable seedling production. Since seed dormancy and germination responses may vary among populations exposed to different climatic and altitudinal conditions, it is necessary to evaluate whether seed origin influences the effectiveness of dormancy-breaking treatments.

Despite these adaptive traits, the natural regeneration of *J. foetidissima* is often limited. The Juniperus species have physical (tough seed coat) and physiological (embryo) dormancy that delays germination, and studies have shown that this makeup plays a major role in seed dormancy (Varsamis et al., 2024). Yucedag et al. (2021) also highlighted in their study that to overcome this delay, a combination of scarification and stratification was needed. This property of the Juniperus species allows its seed to thrive in harsh conditions and allows germination only in optimal conditions, making them optimal candidates for reforestation plans, soil stabilization, and climate-resilient planting (Khalofah, 2022). Boratyński et al. (2025) also highlighted in their study that due to the seed-dormant nature of Juniperus plants, they play vital roles in ecosystem stabilization and erosion control. Irrespective of these potential advantages, this constraint hinders both in situ population renewal and ex situ conservation and afforestation efforts, particularly on degraded calcareous lands.

Therefore, understanding how seed origin and stratification affect germination is important for developing effective propagation protocols for *J. foetidissima*. The present study aimed to evaluate regional variation in seed germination and dormancy of *J. foetidissima* populations from different ecological zones of Azerbaijan and to assess the effect of combined warm–cold stratification on germination percentage, mean germination time, and germination rate.

MATERIALS AND METHODS

J. foetidissima. ripen cones were collected in April 2025 from different regions of Azerbaijan. Topography of Guba-Gusar region is varied, with the lowlands of 500-600 m, and in the Greater Caucasus Mountains, 2000-3000 m. The climate is of moderate continental type with an average temperature of 22-25°C in summer and about -2-3°C in winter; higher altitudes have colder winter and longer snow cover.

This part of Dashkasan-Gadabay region is mostly mountainous with the altitude ranging from about 800-1000 m to 2,000-3,000 m above the sea-level and belongs to the Lesser Caucasus. The region features deep river valleys and forested slopes as well as alpine-subalpine meadows, and the climate is generally mild continental. Summer temperatures average between 18-23°C, while winters range from -3 to -5°C.

The Talysh region has a highly varied relief, with predominantly mountainous landscapes. Elevations range from approximately 0-200 meters in the lowland areas, to 2,000-2,500 meters above sea level in highlands. The region forms part of the Talish Mountains system, characterized by steeply forested slopes and deep river valleys. The climate in the lowland zones is generally humid, subtropical, transitioning to cooler mountain climates at higher elevations. Summer temperatures range from 22-26°C in lowlands, and are milder in mountain areas, around 15-20°C. Winter temperatures are relatively mild in lowlands (approximately 2-5°C), but higher elevations have colder conditions with more snowfall and long-lasting snow cover.

The Nakhchivan region is largely mountainous and marked by sharp contrasts in relief. Elevations range from about 600–800 meters in the valleys to over 3,000 meters in the high mountain areas. It is part of the Nakhchivan Autonomous Republic and is connected to the southern extensions of the Lesser Caucasus. The landscape includes rugged rocky mountains, steep slopes, intermountain depressions, and river valleys mainly associated with the Araz river basin. The climate is predominantly dry continental, with noticeable seasonal differences. Summers are hot and dry; in the lowland areas, average temperatures range between 25–30°C and may rise even higher during peak periods. Winters are relatively cold, with temperatures typically between –3 and –6°C, while higher elevations experience harsher conditions and longer-lasting snow cover.

Subsequently after harvesting the cones, the seeds were manually separated from cones. They were thoroughly cleaned by rinsing with distilled water to remove impurities. In accordance with the method proposed by Tylkowski (2009), the seeds were placed in water to allow the empty seeds to float, while the fully developed seeds were precipitated. The chosen seeds were collected and left to dry under room conditions for 10 days. After drying, 50 fully developed seeds were selected from each of the four studied regions: Guba–Gusar, Dashkasan–Gadabay, the Talysh Mountains, and the Nakhchivan Autonomous Republic. Of these, 25 seeds from each region were used for the stratification treatment, while the remaining 25 seeds served as the control.

Seeds that were collected from the study area were initially placed under warm and moist conditions, maintained at a temperature range of 20–22°C for a period of four weeks to promote primary germination processes. After this warm-moist treatment, the seeds underwent a subsequent cold-moist stratification phase at 4–5°C, which lasted for an additional 10–12 weeks, in order to break dormancy and enhance uniform germination.

After pretreatments seeds were placed in Petri dishes with 1% agar extract.

Each day, germinated seeds were counted, noted and removed from the medium. The experiment was considered complete after the final 20 days elapsed without further germination. A seed was regarded as germinated when the radicle tip appeared from the seed coat (Rzayeva et al., 2026). The main germination parameters measured were: Germination Percentage (GP), Mean Germination Time (MGT) and Mean Germination Rate (MGR). Germination percentage (GP) was determined as follows:

$$GP(\%) = (n\ /\ N) \times 100$$

where n is the number of seeds germinated, and N is the number of seeds sown for germination.

Mean germination time (MGT) and mean germination rate (MGR) were calculated according to Ranal et al. (2009). MGT was calculated using the following formula:

$$MGT = \frac{\sum(n_i \times t_i)}{\sum n_i}$$

where *ni* is the number of seeds germinated at time *ti*, and *ti* is the number of days from the beginning of the experiment to the i-th observation. Mean germination rate (MGR) was calculated as the inverse of MGT:

$$MGR = \frac{1}{MGT}$$

The data were analyzed statistically in Microsoft Excel 2016. The effects of seed origin, stratification treatment and their interaction on germination percentage (GP), mean germination time (MGT) and mean germination rate (MGR) was assessed using the two-way analysis of variance (ANOVA) technique. $p \leq 0.05$ was used as the significance level. Means were compared with Duncan's Multiple Range Test if significant differences were found. The statistically significant differences among means are shown by different lowercase letter in the table.

RESULTS

Table 1 demonstrates the impact of various geographical conditions and cool stratification pretreatment on seed germination characteristics, including Germination Percentage (GP), Mean Germination Time (MGT), and Germination Rate (GR). The obtained results clearly show regional variations in germination performance as a positive response to treatment across all studied areas (DeLuca & Zackrisson, 2007; Emaminasab et al., 2023).

With respect to germination percentage, the highest control result was recorded in the Nakhchivan Autonomous Republic (11.4%), followed by the Dashkasan–Gadabay region (8.2%). Lower germination percentages were observed in the Guba–Gusar (6.4%) and Talysh Mountains (5.3%). And such conditional variations are more likely associated with ecological and climatic differences. Mountainous and relatively humid regions, such as Guba–Gusar and Talysh, may encourage the development of deeper dormancy as an adaptive strategy to prevent premature germination under fluctuating climatic conditions (Gurbanov & Rzayeva, 2019).

In each column mean with the same letter are not significantly different at p<0.0001 Duncus Multiple Range Test (DMRT) GP – Germination percentage, MGT- Mean germination time, MGR – Mean germination rate. According to Duncan's multiple range test ($p \leq 0.05$), germination percentage differed significantly among regions.

The application of mild and cool pretreatment significantly increased germination percentage of seeds from different regions. The greatest enhancement was observed in the Dashkasan–Gadabay population, where GP increased from 8.2% to 14.9%. In the same way, seeds collected from Guba–Gusar and Talysh mountains showed notable progress (from 6.4% to 9.2% and from 5.3% to 7.4%, respectively). Despite the fact that seeds from Nakhchivan Autonomous Republic, previously demonstrated the highest germination level, applied stratification treatment further enhanced germination to 13.1%. These facts suggest that applied pretreatment significantly mitigated dormancy and enhanced seed viability across ecologically different populations.

Mean Germination Time (MGT) values demonstrated a negative correlation with the mild-cool stratification. Under control conditions, the longest germination time was observed in the seeds collected from Talysh Mountains population

Table 1. Seed Germination Parameters (Germination Percentage (GP) mean germination time (MGT) and mean germination rate (MGR) of *Juniperus foetididissima* Willd. from different regions of the Republic of Azerbaijan under control and treatment conditions.

Regions	Germination Percentage (GP)		Mean Germination Time (MGT) (day)		Germination Rate (GR)	
	Control	Treatment	Control	Treatment	Control	Treatment
Dashkasan - Gadabay	8.2^{b}	14.9^{a}	16.25^{c}	10.3^{c}	0.06^{a}	0.10^{a}
Guba - Gusar	6.4^{bc}	9.2^{b}	15.50^{c}	13.6^{b}	0.06^{a}	0.07^{b}
Talysh Mountains	5.3^{c}	7.4^{c}	20.10^{a}	16.8^{a}	0.05^{b}	0.06^{c}
Nakhchivan Autonomous Republic	11.4^{a}	13.1^{a}	18.20^{b}	12.2^{b}	0.05^{b}	0.08^{b}

(20.1 days), followed by Nakhchivan (18.2 days), Dashkasan–Gadabay (16.25 days), and Guba–Gusar (15.5 days). It can be stated that the stratification significantly reduced MGT in all regions, reflecting increased germination rate. The most significant reduction was recorded for seeds from Dashkasan–Gadabay (from 16.25 to 10.3 days), revealing a stronger physiological reaction to treatment. Similarly, there was a significant reduction (18.2 to 12.2 days) in the germination period in Nakhchivan AR.

Germination Rate (GR) measurements provide extra evidence for this trend. In the control conditions, the GR values ranged from 0.05 to 0.06 over the regions which reflects relatively slow germination process. The mild cool stratification treatment resulted in an increase in GR of seeds in all the populations, and maximum GR was observed in Dashkasan-Gadabay (0.10). A moderate growth was registered in Nakhchivan (0.08) and Guba–Gusar (0.07), and a slight, but positive one in Talysh Mountains (0.06). The increase in Germination Rate shows that the stratification treatment had an effect on improving the germination strength and uniformity.

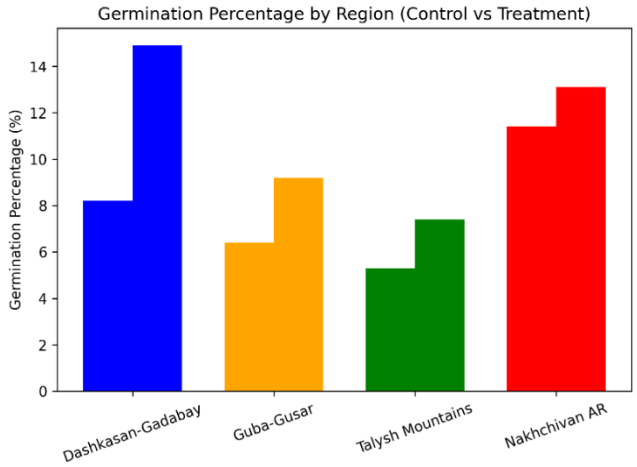


Figure 1. Germination percentage by different region in control and after the stratification treatment.

Generally, regional variations propose that ecological and climatic conditions of seed collected site may influence the initial level of germination potential. The relatively higher germination performance of the Nakhchivan population under control conditions may reflect local adaptation to more continental environments. Conversely, lower germination percentages observed in Talysh and Guba–Gusar populations may be associated with ecological factors promoting stronger dormancy mechanisms.

DISCUSSION

Our results demonstrate distinct regional patterns in seed germination of Juniperus foetidissima. Seeds from the arid Seeds from Nakhchivan and mountainous Dashkasan–Gadabay regions germinated better than those from Talysh and Guba–Gusar, which tend to be more humid and cooler, respectively. In Nakhchivan seeds control germination was 11.4% and in Talysh 5.3%. This implies that seeds from more variable or drier habitats have less dormancy (easier to germinate) and seeds from more consistently moist habitats have more dormancy (more difficult to germinate). The optimum temperature for germination of Mediterranean junipers is cool (5–15°C) and seeds have a "delay mechanism" that prevents germination in a broad cool temperature range in order to prevent erratic rainfalls (Rzayeva et al., 2025; Brink et al., 2020).

The results also show that there was a significant improvement in the germination rate after cold stratification, with Nakhchivan having the highest rate of 13.1%, suggesting that winter-temperature signals are effective in overcoming dormancy. This aligns strongly with Cheng et al. (2022) and Yang et al. (2020), Longer cold stratification greatly enhanced the rate of germination. Seeds that were not stratified, on the other hand, showed little dormancy. These responses reflect other junipers' adaptation; for example, cold stratification speeded up germination in J. communis and other Mediterranean species. In J. foetidissima, stratification also reduced the mean time to germination, leading to more rapid and synchronized germination among populations. In agreement with related species, seeds of J. drupacea germinated quicker following chilling (without significant increase of percent), (Daskalakou et al., 2026), and *J. communis* showed a significant increase in germination only after prolonged cold treatments (Rzayeva et al., 2025).

The differences observed between provenances may be attributed to environmental and/or genetic effects. Populations of J. foetidissima occur in very different climates. Talysh is warm, humid and subtropical, Nakhchivan and Caucasian sites are more continental with severe summer and winter seasons. Studies show that seed characteristics and germination can change to fit the local conditions. Boumediene et al. (2025) found that there was a systematic variation of seed morphology with elevation and aridity; moreover, the variation was mainly caused by the local environment rather than elevation and aridity. Similarly with J. foetidissima, seeds from each area probably have evolved dormancy mechanisms that are appropriate to their mothers' climate. In conifers maternal environmental effects (such as climate at the time of seed maturation) may act as a control of seed dormancy and germination timing that will optimize offspring success in local environments. This also aligns with Klupczyńska and Pawłowski (2021), who repeated the influence of seed dormancy due to the influence of the temperature and origin of seeds during seed development. In this study, no direct genetic data are available for these populations, but the geographically isolated populations of the Caucasus junipers may have distinct genotype or

properties of their seed coats. A low altitude (foggy) provenance may thus have seeds that are already more dormant than a high altitude (dry) provenance, and therefore need a shorter cold period to break dormancy (Gianinetti, 2023; Li et al., 2026).

The findings have important scientific and practical implications. The results show intraspecific functional diversity: within a species, regional gene pools can differ in adaptive traits such as dormancy. This variation is important for understanding theories of plant adaptation and recruitment in heterogeneous landscapes. The results are useful in conservation and forestry practice. Any cold stratification improved the germination, indicating that seed pretreatment needs to be incorporated in propagation protocols for *J. foetidissima*. Cold stratification plus mechanical or acid scarification is expected to yield even better germination based on this study and other work (Gurbanov & Rzayeva, 2025). Indeed, Gurbanov and Rzayeva (2025) suggested that 8 weeks of cold stratification (usually together with scarification) were necessary to overcome deep dormancy.

The results of this study suggest similar protocols for *J. foetidissima*. The use of seeds from a specific region and subjecting them to 1–2 months of cold (5°C) stratification (possibly plus light acid etching) could significantly increase nursery germination. For the restoration of degraded landscapes, it is essential to match the seed provenance to the planting site and also provide adequate seed pretreatment. Due to the low natural regeneration of these junipers, this study provides practical recommendations such as the high-germination provenances (Nakhchivan) can be prioritized for ex situ propagation or at least their responses can be utilized as a reference. More generally, determining the effects of elevation, climate, and genetics on seed traits assists managers in developing strategies for seed collection and storage.

In interpreting this study, several limitations should also be acknowledged. First, the sample size per region was relatively modest and may not represent the full range of intra-population variation in seed dormancy traits. Second, although it was a warm-cold stratification protocol, only one temperature and duration regime were tested. It is unclear whether the optimum stratification conditions might further improve germination, especially for seeds from the Talysh Mountains and Guba-Gusar regions that responded weaker. In addition, the physiological or molecular mechanisms underlying the observed regional differences, such as the levels of endogenous hormones (e.g., abscisic acid and gibberellins) or seed coat impermeability, were not investigated in this research.

Future research should address these gaps by employing larger sample sizes and multiple seed lots per region, testing a range of stratification temperatures and durations, and incorporating viability assays. To confirm natural conditions results, long-term field emergence studies are also required. Lastly, genetic and transcriptomic studies might provide a basis for understanding the adaptive underpinning of dormancy diversity among populations, which could help fine-tune conservation and restoration programmes for Juniperus foetidissima in different landscapes.

Finally, by examining the results in the context of recent research, it is demonstrated that the seed dormancy of J. foetidissima is high but can be influenced by cold and is regionally variable. The knowledge will be used to enhance seedling production and conservation breeding, and to develop reforestation or restoration programs for this ecologically valuable conifer.

***Conclusion*:** In conclusion, the treatment demonstrated a consistently positive effect on germination percentage, germination speed, and germination rate across all studied regions. However, the magnitude of response varied among populations, indicating possible genetic differentiation and ecological adaptation. These findings highlight the importance of considering population origin when developing effective seed pretreatment protocols and restoration strategies.

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***SDGs addressed*:** Climate Action, Life on Land.

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