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## Reproductive trait variability and seed germination responses to electric field and low-dose gamma irradiation in *Larix decidua* Mill.

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### Abstract

*Larix decidua* Mill. (European larch) is an ecologically and economically important deciduous conifer in European mountain ecosystems, whose regeneration success depends on reproductive trait variability and seed physiological quality. Under ongoing climate change, understanding provenance-related differences and identifying effective, environmentally safe pre-sowing treatments are increasingly important. This study assessed the phenotypic variability of cones and seeds across seven geographic provenances of *L. decidua* established in the Baciul seed orchard (Romania) and evaluated seed germination responses to physical stimulation using electric field exposure and low-dose gamma irradiation. Significant differences among provenances were observed for cone morphology and seed biometric traits, including seed weight, size, and number of seeds per cone. Provenances from Sinaia and Brașov V.P. exhibited the highest mean seed weights, while Brașov V.C. produced lighter seeds. Germination experiments showed that electric field treatments significantly enhanced germination, with higher voltages and longer exposure times producing the strongest effects. Low-dose gamma irradiation induced a clear dose-dependent response, with the 2 Gy treatment consistently improving germination percentage, germination index, and early seedling vigor across most provenances. Multivariate analyses (canonical correspondence analysis and UPGMA clustering) revealed distinct provenance-specific physiological responses, with Anina and Sinaia showing divergent reaction patterns, while Gura Humorului, Brașov V.C. and Brașov V.P. formed a more homogeneous group. The results indicate that reproductive trait variability and seed germination capacity in *L. decidua* are strongly influenced by provenance origin and can be effectively modulated by physical pre-sowing treatments, supporting their use in regeneration programs.

**Keywords:** climate adaptation; electric field; genetic resources; seed germination;  $\gamma$  rays' treatments

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## Introduction

Climate change represents one of the most pressing challenges for forest ecosystems globally, with coniferous forests being particularly vulnerable to shifting temperature and precipitation patterns (Ahirvar *et al.*, 2020; Wu *et al.*, 2022; Kabir *et al.*, 2023). Various abiotic stressors, including soil salinity, temperature fluctuations, drought, and soil degradation through erosion, significantly affect plant growth and species distribution in natural ecosystems (Camarero *et al.*, 2024). Soil erosion, recognized as one of the most widespread forms of land degradation globally, can lead to constrained root development, diminished water availability, decreased soil fertility, and altered nutrient dynamics factors that are particularly detrimental during the critical early stages of seedling establishment (Tiebel and Karge, 2025). This highlights the critical protective role of healthy forests, which deliver a multitude of indispensable ecosystem services. Beyond their economic value, forests are vital climate regulators through carbon sequestration, protect water resources and soil stability, purify the air, and sustain biodiversity as well as cultural landscapes (Thompson *et al.*, 2009; Cairns and Meganck, 1994; Sestras *et al.*, 2018; Curovic *et al.*, 2020; Hernández-Blanco *et al.*, 2022; Liu *et al.*, 2024). Temperature stress, in particular, can hinder seedling growth, especially during the early stages of plants' development. Considering these factors, coniferous forests are regarded as particularly vulnerable ecosystems to the effects of climate change (Kurz *et al.*, 2008; Roshani *et al.*, 2022). Understanding how tree species respond to these environmental pressures is useful for developing adaptive management strategies (Chan *et al.*, 2016; Baldrian *et al.*, 2023).

Recent research on Romanian forest species, including those in central and eastern Romania, has revealed significant vulnerability to anticipated climate change scenarios (Crisan *et al.*, 2022; Morar *et al.*, 2023), highlighting the necessity for species-specific assessments and adaptive management strategies across all major forest taxa, including vulnerable conifers like European larch.

*Larix decidua* Mill. (European larch) is an ecologically and economically important coniferous species native to the mountainous regions of Central Europe (Pàques *et al.*, 2013; Vilcan *et al.*, 2013; Kempf *et al.*, 2023). European larch exhibits a discontinuous distribution across the mountain regions of southern, central, and eastern Europe, extending from southeastern France and southwestern Italy, to eastern Poland and central Romania (Albert *et al.*, 2008; Farcas *et al.*, 2013; Wagner, *et al.*, 2015). The species occupies a wide altitudinal gradient, forming continuous forests from approximately 180 m in Poland up to about 2,500 m in the central and southwestern Alps (Milad *et al.*, 2011; Vilcan (Truta) *et al.*, 2017; Teodosiu *et al.*, 2023). At the upper limits of its range, European larch may persist as scattered groups or solitary individuals, particularly in sheltered microsites that mitigate extreme abiotic stress.

Unlike most conifers, *L. decidua* is deciduous, shedding its needles annually, which provides unique adaptations to cold climates and seasonal resource limitations (Tiebel and Karge, 2025). This species is valued for its wood, which is durable and highly sought after in construction, as well as for its ecological contributions to forest ecosystems (Kogelnig-Mayer *et al.*, 2013; Hammond *et al.*, 2022). European larch plays a fundamental role in forest regeneration, soil stabilization, and supporting biodiversity. Similar to silver fir (*Abies alba*), European larch is also affected by the increasing climate change pressures (Zhou *et al.*, 2019; Morar *et al.*, 2023). Larch is widely recognized for its cold climate tolerance, providing it with an advantage in higher altitudes and northern latitudes. However, like other conifer species, it faces challenges from rising temperatures, altered precipitation patterns, and droughts, which can reduce its growth and survival rates. Thus, despite its cold tolerance and wide ecological amplitude, *L. decidua* faces increasing pressures from climate change, particularly regarding altered temperature regimes and water availability (Dobrowolska *et al.*, 2017).

Genetic diversity within forest tree populations is fundamental for adaptation to changing environmental conditions (Mihai and Teodosiu, 2018; Alotaibi *et al.*, 2023). Phenotypic variability in reproductive traits, such as cones and seed characteristics, reflects both genetic differentiation and local

adaptation to specific ecological conditions (Vilcan *et al.*, 2013; Mihai *et al.*, 2019). Studies on seed morphology and cone characteristics provide insights into reproductive strategies, dispersal potential and regeneration success across different environments (Roman *et al.*, 2022a; Arion *et al.*, 2024).

An important factor in preserving and expanding forest ecosystems is the seed germination process, which represents the initial stage of the plant life cycle, where the embryo exits dormancy and initiates active growth. Germination is thus an important phase for plant establishment, as it marks the beginning of a new generation and constitutes a period of high vulnerability for the developing seedling (Choi *et al.*, 2009; Todea *et al.*, 2020). *L. decidua* germination is influenced by a range of internal factors (such as seed viability and nutrient reserves), as well as external conditions (including temperature, moisture, light, and the presence of stimulatory or inhibitory substances).

In the context of climate change and modern silvicultural interventions, understanding the germination process of *L. decidua* and assessing the effects of pre-sowing treatments are increasingly important aspects for improving regeneration efficiency and ensuring the conservation of this valuable species (Li *et al.*, 2021). For larch, elucidating provenance specific variation in cones and seed traits, together with germination behavior, is essential for identifying superior genetic material for reforestation programs and predicting how populations may respond to future climatic scenarios.

Provenance trials, which test the performance of populations from different geographic origins under common environmental conditions, are powerful tools for assessing genetic variation and identifying adapted seed sources (Schiop *et al.*, 2017; Todea *et al.*, 2020; Ciocirlan *et al.*, 2021). The Baciu orchard, established with clonal material from seven natural and artificial *L. decidua* populations across Romania, provides a unique opportunity to evaluate phenotypic variation in cones and seed characteristics, while also considering environmental effects (Plesa *et al.*, 2019; Vilcan (Truta) *et al.*, 2017). Such comparative studies are particularly valuable for species like *L. decidua*, for which research in Romania has been limited compared to other European countries.

As germination is a significant part of the future development of a valuable population as mentioned above, and considering the possibilities to secure optimal results, different approaches were considered. One of the most important physical factors that can be applied in seed treatment and germination enhancement is the electric field (Yang and Shen, 2011; Pauzaite *et al.*, 2018; Česnienė *et al.*, 2023). Germination experiments conducted under different electric current intensities aimed to assess the influence of electrostimulation on seed viability and early germination dynamics, providing new insights into potential methods for improving propagation efficiency and seedling performance (Yang and Shen, 2011; Yudaev *et al.*, 2023). According to Sudsiri *et al.* (2017), electric fields (EF) can enhance not only germination speed, but also final germination percentage, effects that are now being investigated in forestry species of high ecological and economic relevance. Yudaev *et al.* (2023) emphasized that the use of electric treatments in plant production offers several advantages, including low toxicity and minimal surface or groundwater contamination, which in turn contributes to reducing overall production costs in forest nursery systems.

Given the limited information available on the effects of  $\gamma$ -ray treatments on seeds, the present study aimed to evaluate also the influence of low-dose gamma irradiation on the germination of European larch (*L. decidua*) seeds. Gamma irradiation ( $\gamma$ -rays) is one of the most widely used methods for inducing genetic variation in numerous plant species (El-Shakhs *et al.*, 2007; De Micco *et al.*, 2011), including forest trees (Iglesias-Andreu *et al.*, 2012; Geng *et al.*, 2019) and various plant organs. Research on  $\gamma$ -irradiation has also been applied to delay fruit ripening (World Organization of Health and Nutrition in Agriculture, United Nations, 1988), reduce bacterial loads, fungi, insects, and other pathogenic contaminants (Blagojevic *et al.*, 2019; De Rouck, *et al.*, 2025), or improve seed storability (Villegas *et al.*, 2023). Low-dose  $\gamma$ -ray treatments have been reported to stimulate seed germination and increase fruit number and overall yield by up to 86% (Sheppard *et al.*, 1992). Gamma rays can significantly influence seedling growth and development through

genetic, cytological, biochemical, and physiological changes (Kiong et al., 2008), as well as through morphogenetic modifications in cells and tissues, closely linked to the irradiation dose (Blagojevic et al., 2019). Although normally the seed already contains the materials and energy needed for initial growth, certain stimulatory factors are required or beneficial to activate the substances stored in the cotyledons. Low doses of  $\gamma$ -rays may activate enzymes and stimulate the young embryo, enhancing cell division and influencing not only germination, but also the vegetative growth (Piri et al., 2011; Holonec et al., 2021). The biological effects of  $\gamma$ -rays are primarily attributed to the formation of free radicals resulting from water radiolysis, which can modulate the antioxidant system and lead to the accumulation of phenolic compounds and chlorophyll pigments (Wi et al., 2006; Geras'kin et al., 2011; Kondrateva et al., 2019).

Despite the potential of  $\gamma$ -rays to enhance germination performance, relatively few studies have examined their effects on tree species (Iglesias-Andreu et al., 2012). Most forestry research on seed germination has relied on conventional physical or chemical pre-sowing treatments, while low-dose  $\gamma$ -irradiation has been used mainly to generate variation for breeding purposes through induced mutations. It is well established that plant responses to  $\gamma$ -irradiation depend on several factors, including radiation dose, species or genotype, and the specific plant organ under investigation (Esnault et al., 2010; De Micco et al., 2011).

The main objectives of this study were to assess the morphological diversity of cones and seed traits across seven *L. decidua* provenances from the Baciu seed orchard and to determine how these traits relate to germination performance under electric current stimulation and  $\gamma$ -ray treatments. Furthermore, the study aimed to identify provenances exhibiting enhanced reproductive or physiological responses, which may reflect greater fitness or adaptive potential information that is valuable for forest genetic resource management, breeding efforts and climate change adaptation strategies. Maintaining provenance level diversity is fundamental not only for species conservation, but also for maintaining the multiple ecosystem services provided by mountain forests (Arion et al., 2023). By documenting phenotypic variability in key reproductive traits and linking it with germination responses under controlled enhancement treatments, this research supports the conservation and sustainable use of *L. decidua* genetic resources in Romania and Central Europe (Vilcan et al., 2013; Vilcan (Truta) et al., 2017; Gramazio et al., 2018).

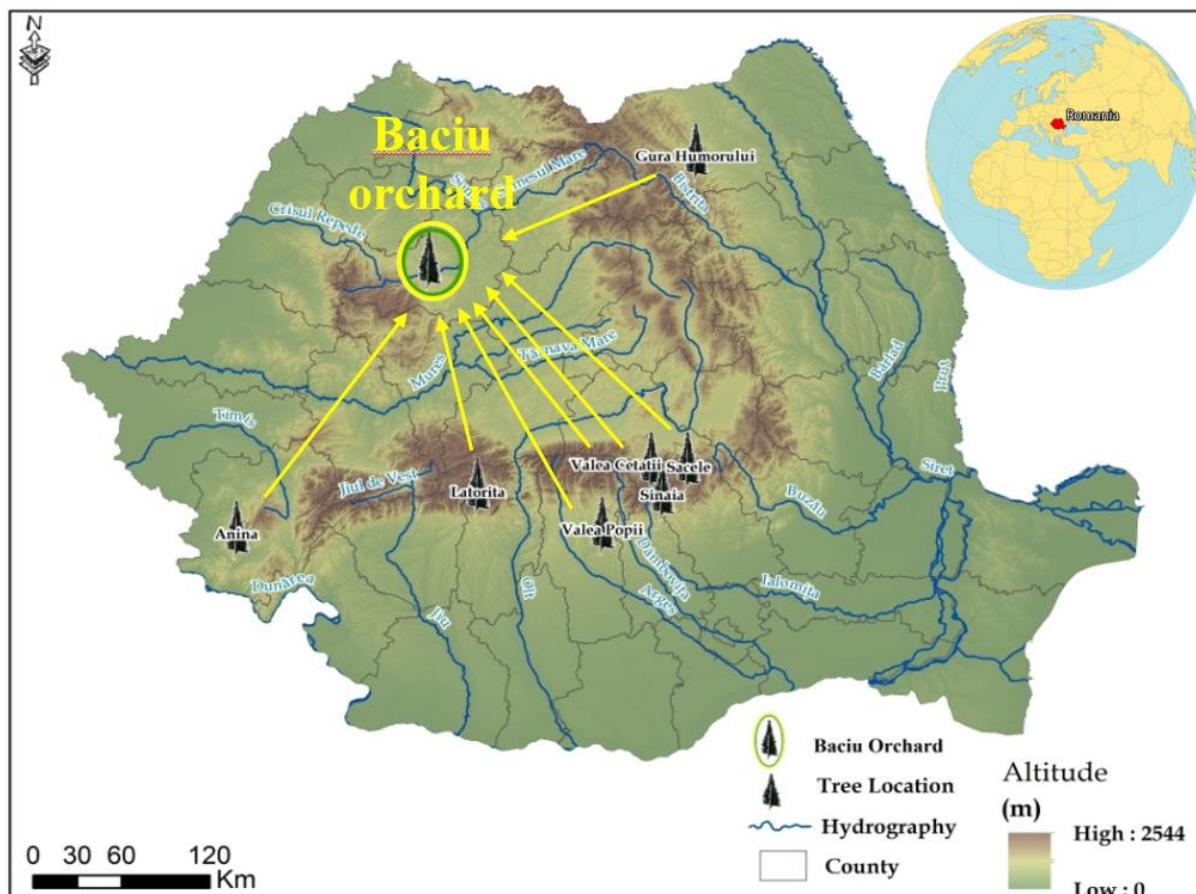
In this context, the present study seeks to clarify how electric fields and low-dose  $\gamma$ -irradiation affect seed germination in European larch, offering new insights that may improve nursery practices and strengthen regeneration strategies for this ecologically and economically important forest species.

## Materials and Methods

### *Geographical distribution of the provenances*

In this study, the biological material consisted of vegetative clones of *Larix decidua* together with the stands from which these clones originated. The clones were produced within a breeding program through the selection of superior individuals from various Romanian geographical regions, belonging to natural or artificial populations: Gura Humorului, Brașov V.C., Săcele, Brașov V. P and Sinaia located in northern Romania, as well as Anina and Latorița situated in the southern part of the country (Figure 1). Plus trees serving as sources of scions were identified within these provenance populations.

The vegetative shoots were grafted onto a uniform rootstock seedling of European larch, resulting in clones, which formed the baseline experimental biological material. These clones were established in the Baciu seed orchard in 1975. The orchard is positioned at 46°8' N latitude and 23°52' E longitude, at an average elevation of 357 m a.s.l. Cones for the present investigation were collected from mature trees (50 years old). For each provenance, cones were harvested from multiple plus trees, to ensure a representative sampling of genetic variation within each origin population. Larch cones were stored indoors for drying, at temperatures of 20-25 °C and the seeds were manually extracted from the dried cones.



**Figure 1.** Location of *L. decidua* origin provenances and Baciu orchard

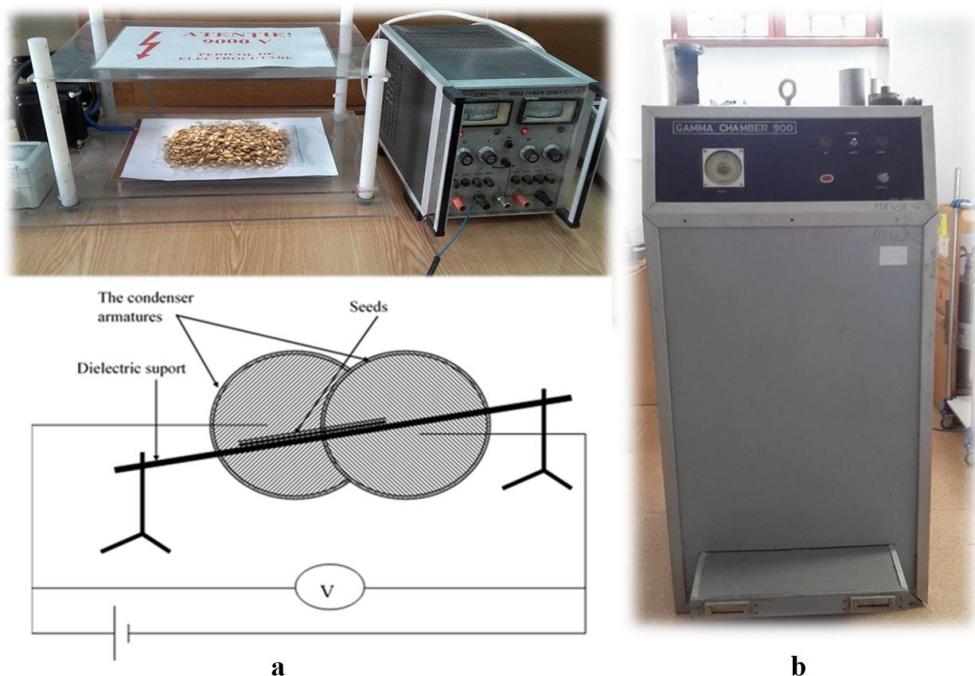
## Characterization of *Larix decidua* Mill. cones and seeds

The main morphometric traits of cones and seeds including cone weight (g), cone length and width (cm), number of seeds/cones and individual seed weight (mg), as well as seed length and width (mm) were thoroughly measured and subsequently correlated with the germination capacity (%). All analyses were conducted in accordance with international ISTA standards and FAO guidelines for the assessment of forest reproductive material quality, and are given as means for each trait/provenance.

### *Seed germination assessment*

### Effect of electric fields treatments on seed germination

The influence of electric fields (EF) on seed germination was investigated at the Biophysical Laboratory of the University of Agricultural Sciences and Veterinary Medicine, Cluj-Napoca, Romania. An EF generator consisting of two electrodes with adjustable spacing, powered by a variable voltage source, was used to expose seed lots. The field intensity was controlled by modifying the distance between the electrodes and the applied voltage. In this experiment, the electrodes were 26 cm diameter and spaced 7.3 cm apart (Figure 2a). Three voltage levels (10 V, 30 V and 50 V) and three exposure durations (15, 35 and 60 minutes) were tested, along with an untreated control.



**Figure 2.** Exposure of larch seeds: (a) electric field; (b)  $\gamma$ -ray

#### *Effect of $\gamma$ -ray treatments on seed germination*

The irradiation of the biological material was conducted at the Atomic and Nuclear Physics Department of Babeş-Bolyai University, Cluj-Napoca. A Gamma Chamber 900 device, using  $^{60}\text{Co}$  as the radiation source, was employed for this study (Figure 2b). The device contains a ring-shaped source with an activity of 900 Curie. Based on literature reports, the following treatments were applied: 1 Gy, 1.5 Gy, 2 Gy and 4 Gy, along with an untreated control. Germination capacity was evaluated based on germination capacity, expressed as the final germination percentage recorded after 30 days. The results provided insights into the role and effectiveness of stimulatory treatments in enhancing the germination rate and assessing the physiological quality of seeds.

#### *Germination parameters of seeds exposed to gamma ray treatments*

Seeds' germination was analyzed based on the main indices (Georgiu *et al.*, 2025):

- GP (Germination percentage - %) (Fetouh and Hassan, 2014):

$$GP = \frac{\text{Number of seeds germinated per day}}{\text{Total number of seeds placed to germination}} \times 100$$

- Global method GI (Germination index) (AOSA, 1983):

$$GI = \frac{\text{Number of germinated seeds}}{\text{Days from the first control}} + \dots + \frac{\text{Number of germinated seeds}}{\text{Days from the last control}}$$

- SE (Germination speed/Germinative energy) (Islam *et al.*, 2009):

$$SE = \frac{\text{Number of germinated seeds in the first day of germination}}{\text{Number of germinated seeds in the last day of germination}} \times 100$$

- CRG (Coefficient of germination speed) (Bewley and Black, 1985; Chiapusio *et al.*, 1997):

$$CRG = \frac{n_1 + n_2 + \dots + n_n}{n_1 \times T_1 + n_2 \times T_2 + n_3 \times T_3 + \dots + n_n \times T_n} \times 100$$

- $n_1$  = number of seeds germinated in day 1 (T1)
- $n_2$  = number of seeds germinated in day 2 (T2)
- $n_n$  = number of seeds germinated in day n (Tn)

#### *Statistical design and data analysis*

The registered data for the seeds were processed as the mean of traits and standard error of the means (SEM). The graphical representation of the relationships between seed traits and germination parameters was based on descriptive and multivariate statistical analyses. ANOVA single factor was considered for data regarding the main traits of seeds and cones. If statistically significant values between averages were registered, the significance test of Tukey was applied ( $\alpha = 0.05$ ) (Sestras, 2018). The data were subjected to a multivariate method, namely canonical correspondence analysis (CCA). A multivariate principal component analysis graph for the seven provenances of larch was created using Past software; the same software was used for the construction of a dendrogram as Euclidean distances among provenances and investigated traits.

## Results

### *Results on the main characteristics of larch cones and seeds*

The results illustrate the variation in cones' characteristics (cone weight, cone length, cone width and the number of seeds/cone) among the seven *L. decidua* provenances: Anina, Latorița, Sinaia, Gura Humorului, Brașov V.C., Săcele and Brașov V.P.

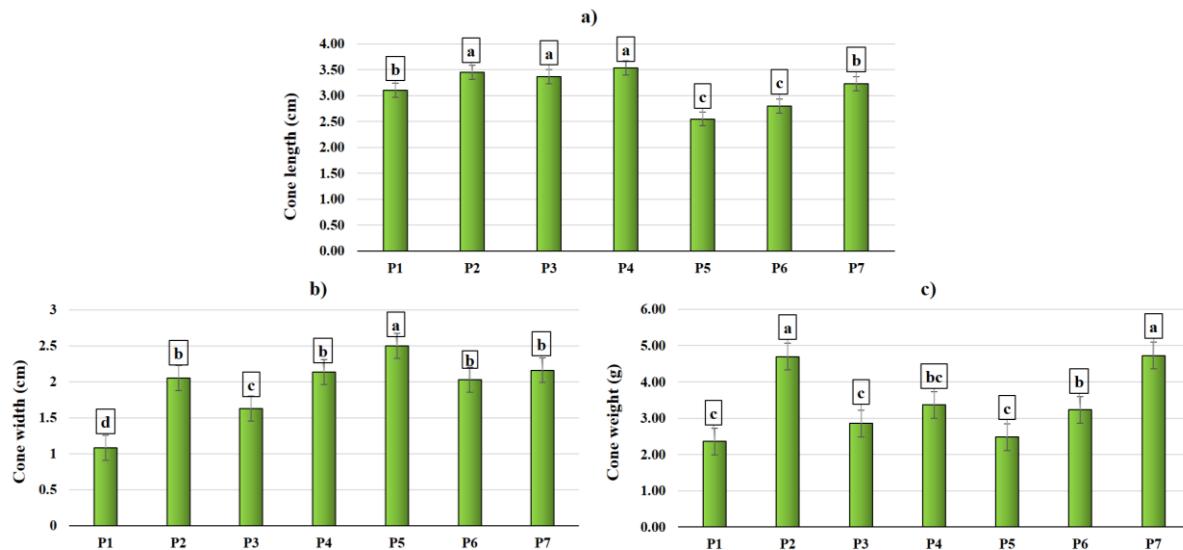
Cone length was the highest in P4 and P2 (Gura Humorului and Latorița respectively, with approximately 3.5–3.4 cm), while P5 (Brașov V.C.) presented the shortest cones (around 2.5 cm). The remaining provenances had intermediate lengths. The higher dispersion of values in Gura Humorului and Latorița provenances indicates a more heterogeneous structure of the respective populations (Figure 3a). Regarding cone width, the widest cones were recorded in P5 (Brașov V.C.) (having 2.5 cm), while P1 (Anina) had narrower cones (1.08 cm). Again, Brașov V.C. displayed greater variability, reflecting a broader range of cone morphologies (Figure 3b). Cone weight showed the highest mean values in the P2 (Latorița) and P7 (Brașov V.P.) provenances (around 4.6 g), indicating better cone development. In contrast, P1 (Anina) exhibited the lowest average cone weight (around 2.4 g), while the other provenances showed intermediate values. The higher variability observed in Latorița and Brașov V.P. populations suggests greater phenotypic diversity (Figure 3c).

The results highlight clear morphological differences among provenances, suggesting that both genetic factors and local environmental conditions influence cones' development in *L. decidua*. Provenances such as Latorița and Brașov V.P. stand out for their higher mean values and variability, while Anina showed smaller cones, potentially reflecting local adaptation or resource limitations. These variations suggest different ecological and genetic adaptations of each provenance, with significant implications for regeneration and seed production.

### *Results on the main characteristics of larch seeds*

The results illustrate a significant variation in seed characteristics (seed weight, seed length, and seed width) among the seven *L. decidua* provenances. Regarding the seed length, the highest value was noticed in P4 (Gura Humorului), with seeds long of around 4.2 mm, indicating well developed seeds, while P6 (Săcele) showed the shortest seeds, of around 3.2 mm. Variability was more pronounced in P4 (Gura Humorului), possibly due to a wider range of environmental influences or genetic heterogeneity (Figure 4a). Seed width

displayed the highest average values (around 2.4 mm), in provenance P3 (Sinaia), whereas P2 (Lătorița) showed the smallest values, of 2.0 mm. The variability across provenances was relatively low, suggesting a consistent trait expression (Figure 4b). Seed weight showed the highest mean values in P3 (Sinaia), with 74.3 mg as a mean for the respective seeds, while P5 Brașov V.C. showed the lowest values, of approximately 54.2 mg. The other provenances studied displayed intermediate seed weights, between 59 and 68 mg. The relatively small variability within each provenance suggests a stable seed size pattern, except for Sinaia provenance, which showed greater dispersion (Figure 4c).



**Figure 3.** The principal traits of the cones, based on the provenances of *L. decidua*

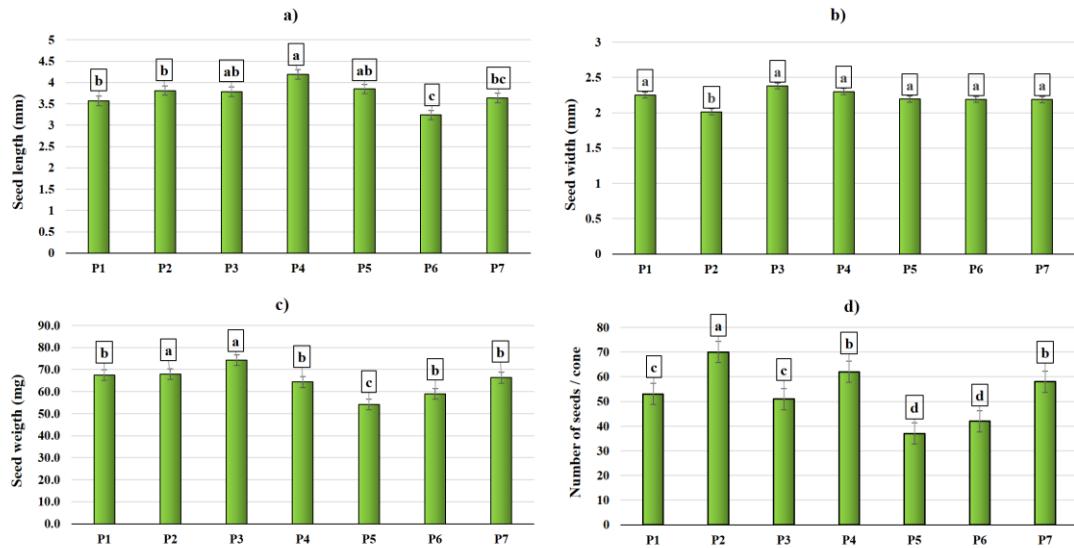
The bars represent the average  $\pm$  SE ( $n = 30$ ). For each character, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ).

P1 (Anina), P2 (Lătorița), P3 (Sinaia), P4 (Gura Humorului), P5 (Brașov V.C.), P6 (Săcele), P7 (Brașov V.P.)

The number of seeds per cone varied significantly among provenances. Provenance P2 (Lătorița) fell within the highest value, having around 70 seeds/cone and indicating a higher reproductive potential, whereas P5 (Brașov V.C.) showed significantly lower number of seeds per cone. These findings underline the substantial reproductive variability among provenances and emphasize the importance of provenance selection in regeneration and seed production strategies (Figure 4d).

According to the literature, larger seeds generally exhibit higher germination rates because they contain a greater reserve of carbohydrates, lipids, and other metabolites that support the initiation of metabolic activity during germination (Kheloufi et al., 2018; Tiebel and Karge, 2025). These enhanced internal resources enable seedlings to sustain early growth processes even under suboptimal environmental conditions, resulting in more vigorous and competitive individuals. Consequently, seed size is often positively correlated not only with germination capacity, but also with subsequent seedling robustness, as larger seeds tend to produce seedlings with greater biomass, improved root development, and higher survival potential in the early stages of establishment (Gorian et al., 2007; Pedrol et al., 2018; Holonec et al., 2021). This relationship underscores the importance of considering seed mass as a key indicator of physiological quality in regeneration and breeding programs.

The hereby results indicate clear morphological differentiation among provenances. Seeds from P3, P2 and P1 (Sinaia, Lătorița and Anina) appear larger and heavier, while P5 (Brașov V.C.) consistently shows smaller and lighter seeds. These differences may reflect once again both genetic variation and local environmental adaptation, influencing seed development and potential germination variation in *L. decidua* populations (Vilcan (Truta) et al., 2017).



**Figure 4.** The principal traits of the seeds, based on the provenances of *L. decidua*

The bars represent the average  $\pm$  SE ( $n = 30$ ). For each character, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ).

P1 (Anina), P2 (Latorița), P3 (Sinaia), P4 (Gura Humorului), P5 (Brașov V.C.), P6 (Săcele), P7 (Brașov V.P.)

The morphological features noted in the seeds of different forest species underscore the significance of their origin (Roman *et al.*, 2022a). Similar studies have been conducted, emphasizing the relevance of understanding reproductive traits and genetic diversity across different populations (Vilcan (Truta) *et al.*, 2017; Gramazio *et al.*, 2018; Todea *et al.*, 2019; Roman *et al.*, 2022b). These studies are important as they offer valuable insights into how populations adapt to their specific environments and interact with other species within their ecosystems. Gaining knowledge about reproductive traits can guide conservation efforts, especially in the face of environmental changes and habitat degradation. Additionally, genetic diversity plays a vital role in enhancing a population's ability to withstand abiotic stress and adapt to shifting climatic conditions.

#### Results on germination capacity after exposing seeds in EF

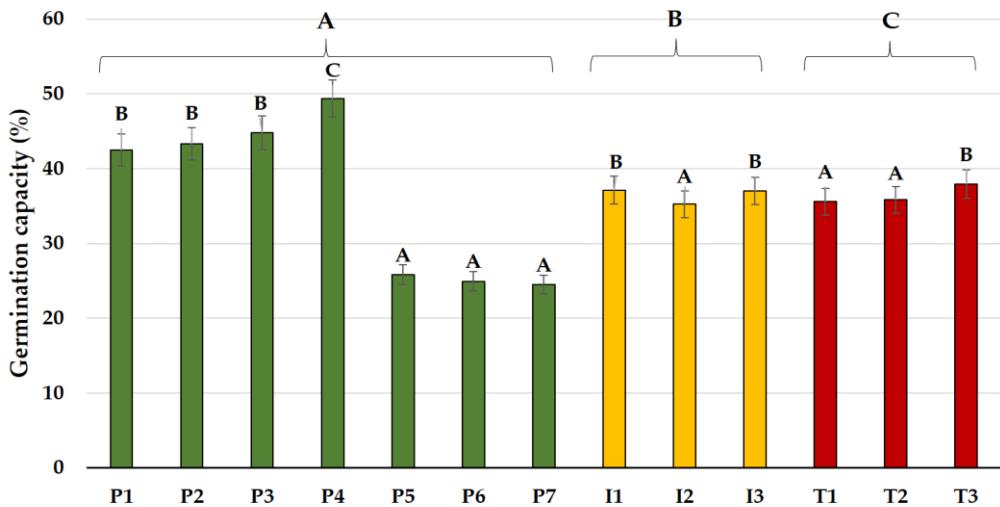
The germination capacity of *L. decidua* varied significantly among provenances, electric field intensities and timing intervals (Figure 5). Among all the studied provenances (P1–P7), the highest germination percentages were recorded for P4 and P3, whereas P7 and P6 showed significantly lower germination capacities (hereafter referred to as group A), indicating a reduced physiological performance under the tested conditions.

Regarding the effect of electric field intensity, germination increased progressively with field strength. Seeds exposed to 10 V (I1) and 50 V (I3) exhibited significantly higher germination percentages (group "B") compared with the 30 V treatment (I2), which consistently remained in the lower statistical group. This pattern suggests a positive stimulatory effect of higher electric intensities on seed activation.

Similarly, the timing intervals produced significant differences. The longest exposure, T3 (60 min), resulted in higher germination values (group "C"), whereas shorter durations (T1 = 15 min and T2 = 35 min) were grouped under the lower category. These outcomes indicate that prolonged exposure enhances the physiological response to the electrical treatment. Regarding the interaction between provenance, electric field intensity and treatment duration reveals that higher voltages combined with longer exposure times substantially improve germination performance, while seeds from weaker-performing provenances remain less responsive overall (Figure 5).

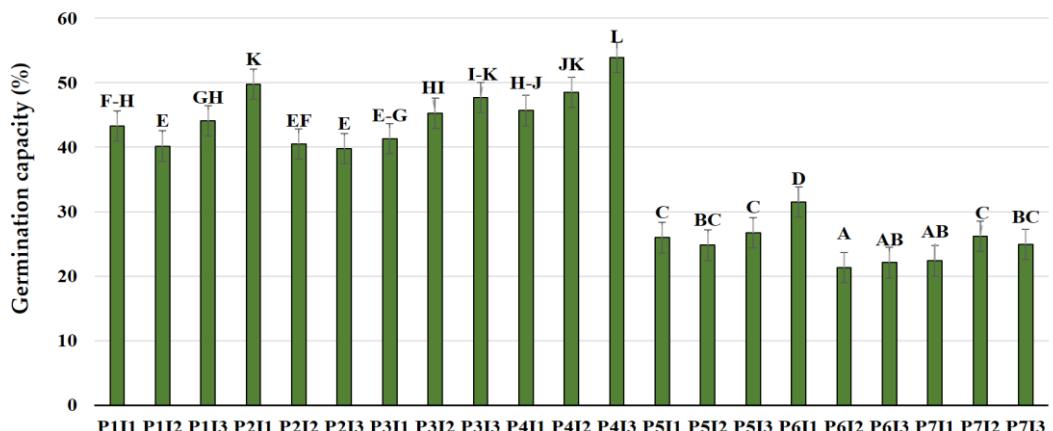
Statistically significant differences were observed in the interaction between provenance and electric field intensity. This indicates that the germination response of seeds is influenced not only by the applied EF intensity, but also by the genetic origin of the seed material. The highest germination was recorded for P4I3,

followed by P2I1, while the lowest was observed for P6I2. The findings indicate that some provenances are more sensitive, while others exhibit greater tolerance to variations in electric field intensity, emphasizing that the treatment's effects are influenced by the unique genetic and physiological traits of each provenance (Figure 6).



**Figure 5.** The effects of electric field intensity on *L. decidua* germination capacity (%) for provenance (A), intensity (B) and exposure time (C)

The bars represent the average  $\pm$  SE ( $n = 30$ ). For each factor, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ). P1 (Anina), P2 (Latorița), P3 (Sinaia), P4 (Gura Humorului), P5 (Brașov V.C.), P6 (Săcele), P7 (Brașov V.P.); I1 = 10V, I2 = 30V, I3 = 50V; T1 = 15 min, T2 = 35 min, T3 = 60 min.



**Figure 6.** Germination capacity (%) of *L. decidua*, depending on the interaction between provenance and electric field intensity

The bars represent the average  $\pm$  SE ( $n = 30$ ). For each factor, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ). P1 (Anina), P2 (Latorița), P3 (Sinaia), P4 (Gura Humorului), P5 (Brașov V.C.), P6 (Săcele), P7 (Brașov V.P.); I1 = 10V, I2 = 30V, I3 = 50V

The interaction between provenance (P) and exposure time (T) was noted, indicating that the temporal dynamics of larch seed germination are affected by the genetic origin. This implies that various provenances demonstrate unique germination patterns over time, reflecting their intrinsic genetic and physiological characteristics that influence their response throughout the experimental period. The highest germination rates were recorded for P4T3, followed by P4T1 and P4T2, while the lowest was observed in P5T1 (Figure 7).

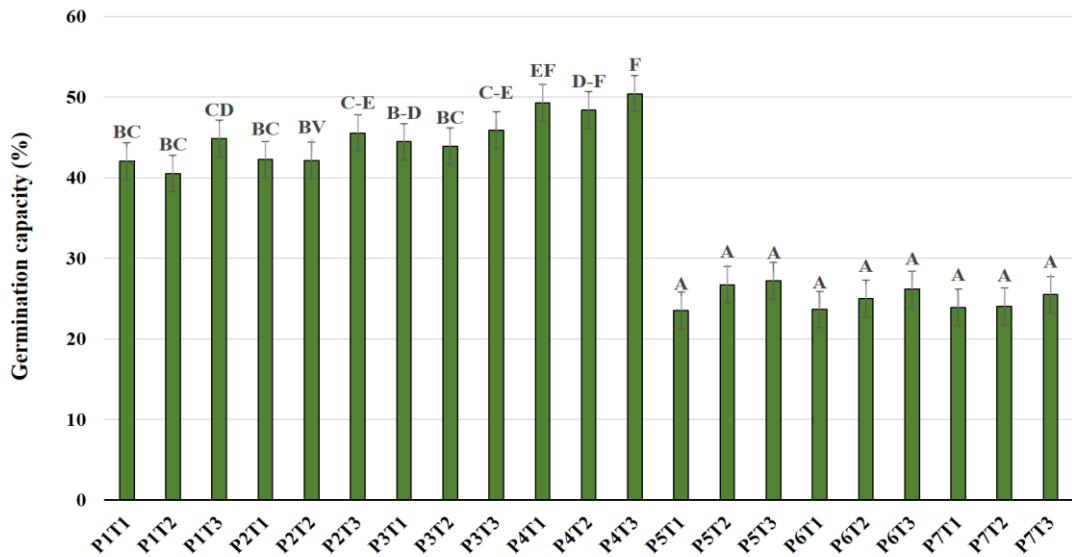


Figure 7. Germination capacity (%) on *L. decidua* depending on the interaction between provenance and EF exposure time

The bars represent the average  $\pm$  SE ( $n = 30$ ). For each factor, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ). P1 (Anina), P2 (Lăzărești), P3 (Sinaia), P4 (Gura Humorului), P5 (Brașov V.C.), P6 (Săcele), P7 (Brașov V.P.); T1 = 15 min, T2 = 35 min, T3 = 60 min.

The interaction between time (T) and electric field intensity (I) was observed, indicating that the temporal dynamics of larch seed germination are influenced by the applied treatment. This suggests that different intensities elicit distinct germination patterns over time, reflecting the inherent physiological and genetic traits of the seeds. Consequently, certain combinations of time and intensity promote higher germination rates, while others result in lower performance. The highest germination was recorded for T3I1, followed by T3I3, whereas the lowest was observed for T1I2 and T2I2, highlighting the importance of optimizing both the duration and EF intensity to maximize the germination potential of larch seeds (Figure 8).

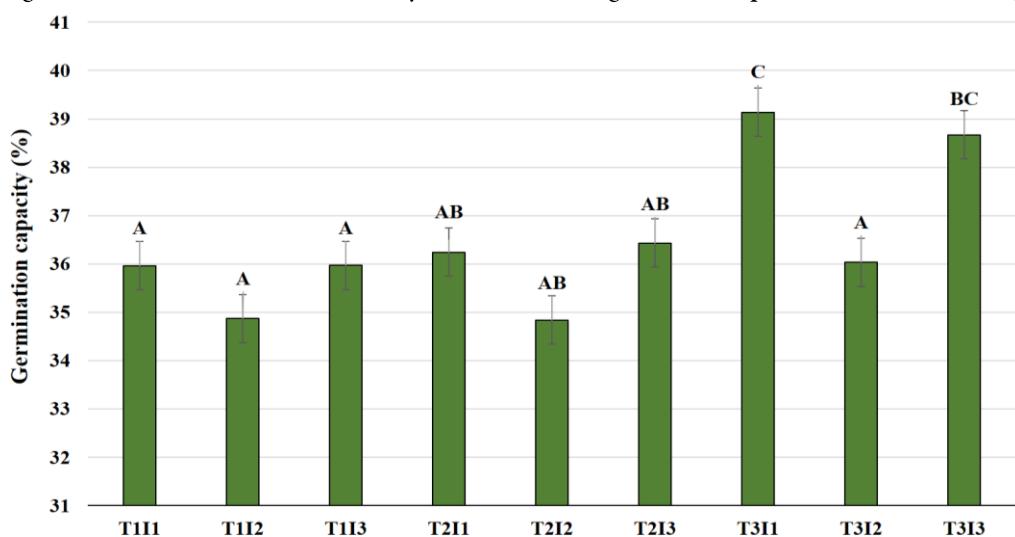


Figure 8. Germination capacity (%) on *L. decidua* depending on the interaction between exposure time and EF intensity

The bars represent the average  $\pm$  SE ( $n = 30$ ). For each factor, different letters from top of bars indicate significant differences between treatments, according to Tukey's test ( $\alpha=0.05$ ). T1 = 15 min, T2 = 35 min, T3 = 60 min; I1 = 10V, I2 = 30V, I3 = 50V

*Results on germination capacity after exposing *L. decidua* seeds to  $\gamma$  rays*

The variation within the germination indices (Table 1) highlighting the impacts of seed provenance and gamma irradiation treatments. This data illustrates how seed origin and exposure to gamma radiation can significantly affect germination rates and related metrics.

**Table 1.** The main germination indices depending on the provenances of *L. decidua* and the influence of the  $\gamma$  ray treatments on seed germination capacity (%)

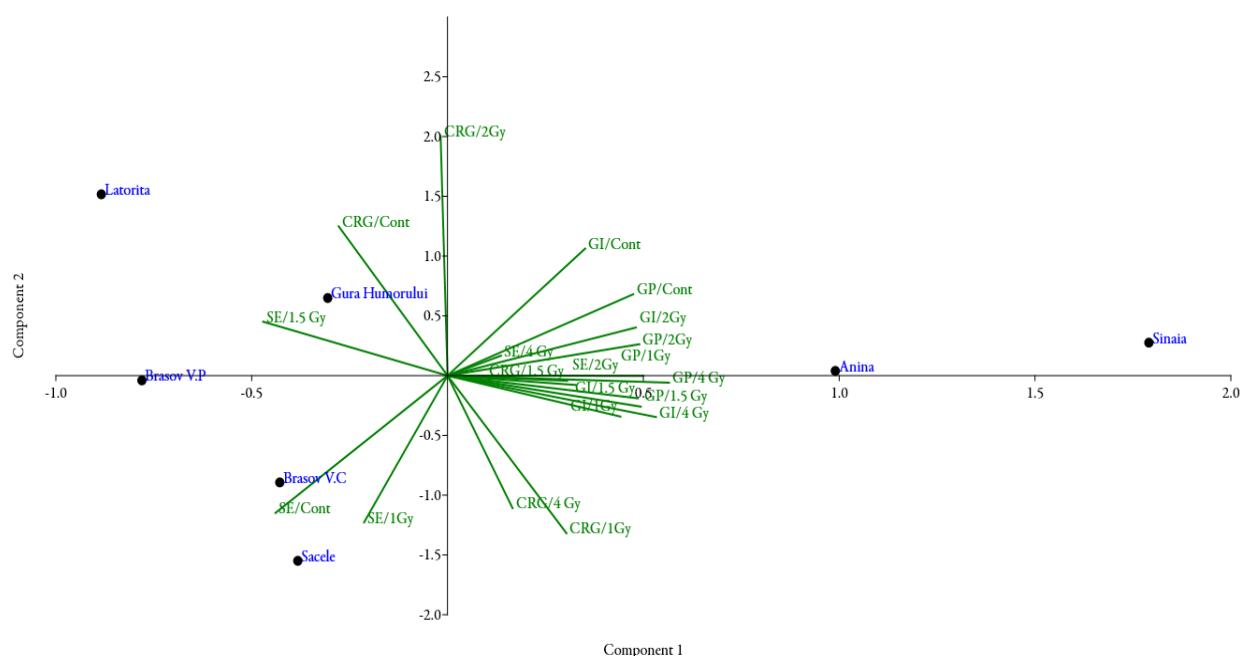
No	Treatment/Provenance	Germination indices			
		GP	GI	SE	CRG
Control (no treatment)					
1	Anina	46.67	1.08	7.10	7.65
2	Lătorița	40	1.04	8.30	7.84
3	Sinaia	53.33	1.21	6.30	7.39
4	Gura Humorului	40	0.93	8.30	7.80
5	Brașov V.C.	33.33	0.73	10	7.586
6	Săcele	36.67	0.88	9.1	7.33
7	Brașov V.P.	36.67	0.9	9.1	8.03
1 Gy					
1	Anina	43.33	0.94	7.7	7.93
2	Lătorița	30	0.59	11.1	6.72
3	Sinaia	50	1.1	6.7	7.41
4	Gura Humorului	36.37	0.76	9.1	7.04
5	Brașov V.C.	33.3	0.71	10	7.44
6	Săcele	33.3	0.8	20	7.58
7	Brașov V.P.	36.67	0.83	9.1	7.1
1.5 Gy					
1	Anina	50	1.13	6.7	7.85
2	Lătorița	36.67	0.85	9.1	7.01
3	Sinaia	60	1.35	5.6	7.33
4	Gura Humorului	43.3	1.06	7.7	7.39
5	Brașov V.C.	43.33	0.98	7.7	7.41
6	Săcele	43.33	1	7.7	7.1
7	Brașov V.P.	40	0.88	8.3	6.86
2 Gy					
1	Anina	66.67	1.64	5	7.41
2	Lătorița	60	1.41	5.6	7.69
3	Sinaia	73.33	1.78	9.1	7.35
4	Gura Humorului	56.67	1.41	5.09	7.66
5	Brașov V.C.	56.67	1.38	5.9	7.39
6	Săcele	60	1.37	5.7	7.06
7	Brașov V.P.	53.33	1.24	6.3	7.17
4 Gy					
1	Anina	56.67	1.46	17.6	7.87
2	Lătorița	43.33	0.99	7.7	7.1
3	Sinaia	63.33	1.59	5.3	7.66
4	Gura Humorului	46.67	1.16	7.1	7.73
5	Brașov V.C.	46.67	1.22	7.1	8
6	Săcele	46.67	1.15	7.11	7.53
7	Brașov V.P.	43.33	1.07	7.7	7.65

\* GP-germination percentage, GI-germination index, SE-speed of emergence, CRG-coefficient of germination speed

Four key biological parameters were assessed: germination percentage (GP), germination index (GI), speed of emergence (SE), and coefficient of germination speed (CRG). The dataset was structured into five experimental groups: the untreated control and irradiation doses of 1 Gy, 1.5 Gy, 2 Gy and 4 Gy. Within the control group, GP values ranged from 33.33% to 53.33%, indicating inherent differences among provenances in their baseline germination capacity (Table 1).

The GI, SE, and CRG values characterize the natural germination dynamics and serve as reference points for evaluating treatment effects. Gamma irradiation induced distinct modifications depending on both the dose and the seed provenance. At 1 Gy, a slight reduction in GP and GI was observed for several provenances, suggesting an initial sensitivity to low-dose irradiation. At 1.5 Gy, the germination response became more heterogeneous, with some provenances showing increased GP and GI values, while others exhibited moderate inhibitory effects. The 2 Gy treatment produced the most pronounced stimulatory effects, reflected by increased GP and GI values across most provenances, including maximum recorded values (up to 73.33% GP for the Sinaia provenance). This dose appears to enhance both germination capacity and vigor. At 4 Gy, the response was more variable: some provenances maintaining relatively high germination indices, whereas others show declines, indicating differences in physiological tolerance thresholds (Table 1). The dataset highlights a dose-dependent and provenance-specific germination response, emphasizing the role of genetic variability in irradiation tolerance and suggesting that moderate gamma doses may act as effective stimulants for *L. decidua* seed germination. Understanding these variations is necessary for optimizing germination and enhancing the growth potential of *L. decidua* in various ecological conditions.

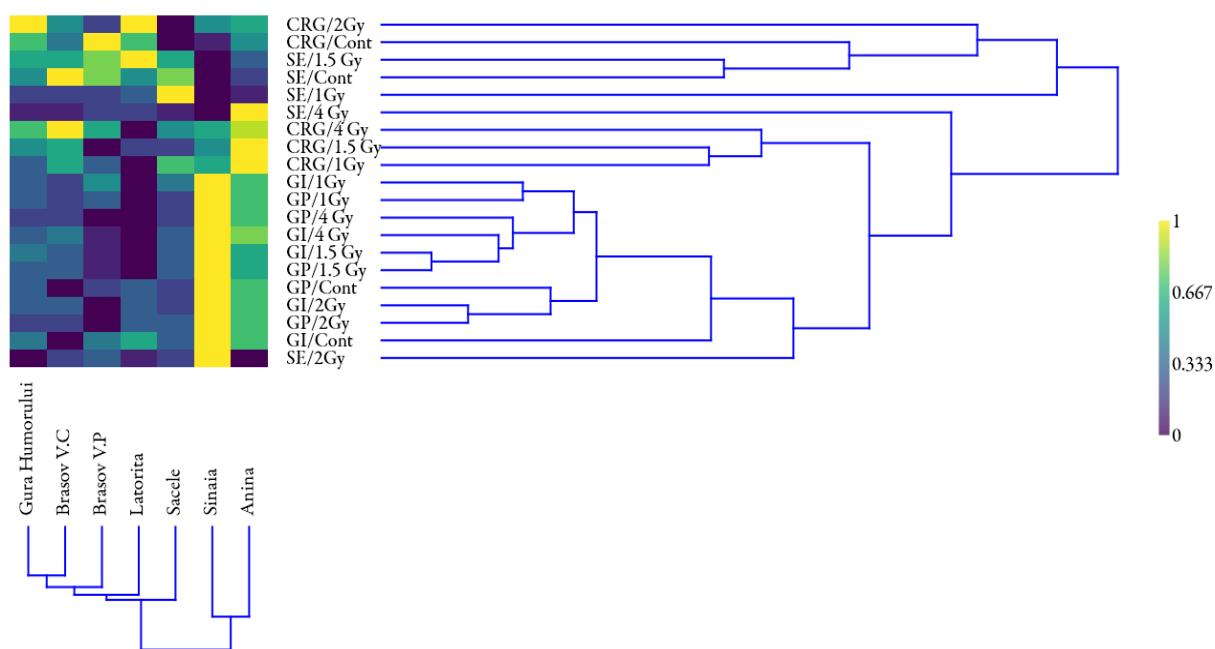
Canonical correspondence analysis (CCA) is a multivariate method useful for elucidating and representing the relationships between biological assemblages of species and their environment (Ter Braak and Verdonschot, 1995). In this study, seeds traits, germination treatments with  $\gamma$  ray and provenance of origin were analyzed and correlated in this regard. The CCA analysis reveals clear differences among the *L. decidua* provenances in their responses to  $\gamma$ -irradiation, outlining two main groups: Anina, Sinaia, which were predominantly associated with GP and GI treatments (including higher doses) and the group formed by Brașov V.P., Brașov V.C., Săcele and Latorița, which were more closely linked to SE and CRG treatments, while Gura Humorului exhibited an intermediate response (Figure 9).



**Figure 9.** Canonical correspondence analysis (CCA) for the seven *L. decidua* provenances and the influence of  $\gamma$  ray treatments on the germination capacity

The results indicate that the intensity and type of  $\gamma$ -ray treatment generate distinct physiological or genetic reaction patterns among provenances, relevant for selection strategies. This suggests that  $\gamma$ -irradiation treatments reveal meaningful provenance-level variability that can inform future breeding and resilience programs.

The dendrogram in Figure 10 represents the clustering of treatments according to their germination response. Two major clusters can be observed (right side): one group that includes predominantly the control variants and moderate treatments, and a second group that comprises mainly the applied treatments showing similar effects induced by higher radiation doses. This pattern suggests a phenotypic convergence among some provenances regardless of treatment, while simultaneously revealing a clear separation for other provenance dose combinations. The dendrogram also reflects the similarity relationships among the seven larch provenances. Its structure indicates a functional proximity between origin such as Gura Humorului, Brașov V.C. and Brașov V.P., whereas Anina and Sinaia are distinguished by a greater distance from the other populations. This separation suggests the presence of genetic or ecological particularities influencing the germination response to irradiation. The figure illustrates how intraspecific variability and gamma-ray treatments interact to shape germination capacity in *L. decidua* and the UPGMA analysis based on the Gower similarity index provides a robust perspective on the relationships among provenances and treatments (Figure 10).



**Figure 10.** Hierarchical clustering-paired group UPGMA (unweighted pair group method with arithmetic mean)-similarity index (Gower) of the seven *L. decidua* provenances and the influence of the  $\gamma$  ray treatments on the germination capacity

The multivariate analyses employed UPGMA based on the Gower similarity index and Canonical Correspondence Analysis (CCA) consistently reveal a well-defined pattern of inter- and intra-provenance variation of *L. decidua* germination response in relation to gamma-ray treatments. The UPGMA dendrograms highlight stable groupings among certain provenances (Gura Humorului, Brașov V.C., Brașov V.P.), while others (Anina, Sinaia) exhibit distinct behavior, pointing to underlying ecological or genetic differentiation.

## Discussion

The analysis of seed traits revealed pronounced differences among the seven *L. decidua* provenances. The results indicate distinct morphological divergence, suggesting that both genetic background and local environmental conditions play a central role in shaping larch cone development. Provenances such as Lătorița and Brașov V.P. are characterized by higher mean trait values and greater variability, whereas Anina exhibits smaller cones, a pattern that may reflect localized adaptation processes or resource constraints. These findings highlight the existence of differentiated ecological and genetic strategies among provenances, with direct implications for natural regeneration dynamics and seed production potential. Similarly, the morphological assessment of seeds confirms clear provenance-specific differentiation. Seeds originating from P3, P2 and P1 (Sinaia, Lătorița and Anina) tend to be larger and heavier, while P5 (Brașov V.C.) consistently presents smaller and lighter seeds. Such variation likely reflects the combined influence of genetic divergence and environmental selective pressures, factors that collectively shape seed development and may ultimately affect germination performance in *L. decidua* populations (Stoehr, 2000; Vilcan (Truta) *et al.*, 2017; Iralu *et al.*, 2019).

The observed morphological patterns align with previous findings in other forest species, where seed origin has been consistently identified as a critical determinant of reproductive traits (Colas *et al.*, 2008; Matsushita *et al.*, 2020; Roman *et al.*, 2022a). Comparable investigations conducted on larch and related taxa further emphasize the importance of understanding population-level variation in reproductive characteristics and genetic diversity (Schiop *et al.*, 2017; Chen *et al.*, 2018). These studies provide valuable insights into how forest populations adapt to their specific environmental contexts and interact within their ecological networks. Moreover, knowledge of reproductive traits and genetic variability is essential for guiding conservation strategies, particularly in the context of environmental change and habitat degradation (Todea *et al.*, 2019). Genetic diversity enhances population resilience by improving tolerance to abiotic stressors and facilitating adaptive responses to shifting climatic conditions.

The current findings emphasize that seed size and morphology are provenance-dependent traits influenced by both genetic factors and local environmental conditions. Such information is critical for selecting appropriate provenances for seed collection, seedling production, and forest regeneration programs, ensuring both high germination success and the maintenance of genetic diversity within *L. decidua* populations.

Regarding the germination capacity, the results of this study clearly demonstrate that the germination of larch seeds is influenced by both genetic origin (provenance) and the applied experimental treatments, namely time and electric field intensity in this case. The statistically significant interactions observed between provenance and EF intensity, provenance and exposure time, indicate that the response of larch seeds is not uniform, but rather shaped by a combination of intrinsic genetic traits and external factors. Certain provenances, such as P4, showed higher sensitivity to the applied electric field, achieving the highest germination rates under specific combinations of time and intensity (T3I1). In contrast, other provenances, such as P5 and P6, exhibited lower tolerance, reflected in reduced germination under less favorable conditions (T1I2). This variability underscores the importance of considering provenance when designing pre-sowing treatments, as genetic and physiological differences can markedly influence the effectiveness of these interventions.

The use of electric fields (EF) has been associated with several advantages, including low toxicity and minimal risk of soil or groundwater contamination (Vasilevski, 2003). Although several studies have reported positive effects of high-voltage treatments on yield and growth parameters in various species, similar approaches have increasingly been explored for forest tree species such as *Sorbus pohuashanensis* (Yang and Shen, 2011), *Picea abies* (Singorzan *et al.*, 2022), *Quercus robur* (Holonec *et al.*, 2021), *Fagus sylvatica* (Česnienė *et al.*, 2023) or *Elaeis guineensis* (Sudsiri *et al.*, 2017). Similarly, Lynikeine *et al.* (2006) found that EF exposure not only increased germination rates, but also improved the overall germination performance of various horticultural taxa.

Our findings are consistent with these observations. In the present study, exposing the larch seeds to an EF for 60 minutes resulted in the highest germination increase. Shorter exposure durations of 15 and 45 minutes also produced notable improvements, enhancing germination. These results suggest that EF stimulation can act as an effective pre-sowing treatment for *L. decidua*, with longer exposure times producing stronger stimulatory effects. Moreover, the consistency between our results and previous studies reinforces the potential applicability of EF treatments in forestry practices and seed-enhancement technologies.

The CCA results reinforce this separation: most provenances cluster near the origin, indicating a relatively uniform and moderate response to varying  $\gamma$ -irradiation doses, whereas Anina and Sinaia are positioned at large distances along the first canonical axis, suggesting a specific sensitivity or distinct reactivity to the treatments. The irradiation vectors show subtle, structured differences among doses, but no single dominant direction, indicating a complex, provenance-dependent response.

Integrating the two analyses demonstrates that the germination response of *L. decidua* provenances is shaped by both their genetic identity and the intensity of  $\gamma$ -irradiation, although the provenance effect exhibits stronger structuring than the treatment effect. Notably, the provenances Anina and Sinaia consistently stand out through distinct germination behavior, suggesting that breeding strategies or tolerance-testing programs involving irradiation should account for these origin-specific differences.

From a practical silvicultural perspective, these findings highlight the necessity of tailoring pre-sowing treatments to the specific characteristics of the seed material. Optimizing both the intensity of the electric field and the duration of exposure can enhance germination success, particularly for provenances with inherently higher responsiveness. Such optimization is necessary for improving the efficiency of larch seedling production and ensuring the establishment of genetically diverse and resilient forest stands.

In conclusion, the study confirms that both genetic origin and treatment conditions interact to determine the germination outcomes of larch seeds. Future research should explore the underlying physiological mechanisms and extend these findings to field conditions, enabling the development of provenance specific protocols that maximize germination and early growth performance.

## Conclusions

This research highlights the substantial influence of provenance and physical presuming treatments on the reproductive traits and germination performance of *L. decidua*. The seven provenances studied exhibited clear morphological differentiation in cones and seed characteristics, reflecting both genetic diversity and adaptation to their native environmental conditions. Germination experiments revealed that enhancement treatments based on electric fields and low-dose  $\gamma$ -irradiation significantly modulate germination capacity. Electric field exposure, particularly at higher intensities and longer durations, consistently improved germination, demonstrating its potential as a low-toxicity, environmentally safe stimulation method. Similarly,  $\gamma$ -irradiation produced a dose-dependent response, with the 2 Gy treatment yielding the most pronounced improvements in germination indices across multiple larch provenances. These effects were further supported by the multivariate analyses (CCA and UPGMA), which identified distinct physiological reaction patterns. The study demonstrates that both intrinsic genetic factors and external stimulatory treatments play essential roles in shaping germination outcomes in *L. decidua*. The observed provenance dependent responses emphasize the necessity of selecting suitable seed sources for regeneration programs, while the positive effects of EF physical treatments suggest practical opportunities for improving seedling production without relying on chemical inputs. These findings provide valuable guidance for forest managers, seed orchard specialists, and breeding programs aiming to enhance regeneration efficiency, maintain genetic diversity, and support climate-resilient management of European larch populations.

### Authors' Contributions

Conceptualization: P.T., A.M.T. and L.D.; Data curation: I.M.M., C.D. and I.D.A.; Formal analysis: P.T., I.M.M., A.M.T., C.D. and O.V.; Funding acquisition: P.T., A.M.T. and O.V.; Investigation: P.T., I.M.M., A.M.T. and A.F.S.; Methodology: A.M.T., I.D.A., F.I. and A.F.S.; Project administration: P.T. and L.D.; Resources: P.T., O.V. and L.D.; Software: P.T., I.M.M., A.F.S., and L.D.; Supervision: A.F.S. and L.D.; Validation: F.I., A.F.S. and L.D.; Visualization: L.D. and F.I.; Writing - original draft: P.T., I.M.M., C.D. and A.M.T.; Writing - review and editing; F.I., A.F.S. and L.D.

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### Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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