https://doi.org/10.17221/46/2025-PSE

Seed germination strategy as an indicator of suitability for restoration of species-rich meadows

Faisal Anggi Pradita, Maria Janicka*

Agronomy Department, Agriculture Institute, Warsaw University of Life Sciences, Warsaw, Poland
**Corresponding author: faisal_pradita@sggw.edu.pl*

Citation: Pradita F.A., Janicka M. (2025): Seed germination strategy as an indicator of suitability for restoration of species-rich meadows. Plant Soil Environ., 71: 353–362.

Abstract: Restoration of *Arrhenatherion* meadows is limited both by the lack of local seed availability in natural habitats for self-restoration purposes and the lack of information on the germination of target species in these meadows. Understanding germination strategies can optimise local seed use. This study aimed to define germination strategies for groups of species based on relevant six germination parameters: germination capacity (GC), fresh ungerminated seed (FUS), median germination time, germination velocity, germination synchrony and germination uniformity. The germination test of 23 meadow species was performed according to ISTA (International Seed Testing Association) rules. The hierarchical clustering method and PCA biplot divided the species into five groups. Based on the Kruskal-Wallis and Dunn's test, the evaluation of six parameters in five groups showed that species such as *Arrhenatherum elatius*, *Centaurea jacea*, *Plantago lanceolata*, *Tragopogon pratensis* and *Dianthus deltoides* differed significantly in terms of higher GC, lower FUS and faster germination velocity than *Lathyrus pratensis*, *Vicia angustifolia* and *Geranium pratense*. Conversely, these three species had more synchronous germination than species such as *Knautia arvensis* and *Briza media* and expressed the shortest peak of germination period among other species. These six parameters potentially describe germination strategies across groups of species.

Keywords: floristic diversity; germinability; lowland hay meadows; semi-natural meadows; temperate grasslands

The European Union has set the goal of increasing protected areas to at least 30% of its land and sea surface by 2030 by increasing biodiversity and restoring species-rich communities such as lowland hay meadows (European Commission 2021). The use of local seeds has been prioritised as a part of conservation since such seeds capture the same genetic diversity of restored areas. However, the availability of these seeds in nature is scarce (Pedrini et al. 2020). Climate change also threatens the establishment of local species by reducing seed production from the remaining vegetation and decreasing the seeds' germinability (Veselá et al. 2020). Germination is the first step to ensure plant coexistence (Nonogaki et al. 2010). Therefore, assessing seed germination capacity prior to sowing is crucial for predicting restoration success, while germination testing is a key method for this assessment (Kildisheva et al. 2020).

However, due to the wide range of germination requirements of local species, assessing the number of germinating seeds as a single parameter in a germination test often fails to predict the re-establishment of plant communities (Seglias et al. 2018). This is due to the influence of functional traits such as dormancy, seed mass, life cycle and life form controlling germination (Kildisheva et al. 2020). Interactions between these traits can create heterogeneity in germination strategies, potentially leading to misinterpretation by assessing only the germination percentage (Zhao et al. 2021). For these reasons, Ranal and Santana (2006) recommended assessing multiple germination parameters for timing, number of germinated seeds, and germination uniformity to describe germination performances. In addition, differences in germination performances among grassland plants generate specific patterns characterising the germination strategy

https://doi.org/10.17221/46/2025-PSE

(Zhang et al. 2021). Understanding the germination strategies of species can inform ecological practices such as determining collection times and sowing management (Hay and Probert 2013).

This study can contribute to bridging the knowledge gap by developing germination strategies by assessing multiple germination parameters that are still not well observed in species of *Arrtenatherion* meadows. The study examines the hypothesis that different species exhibit distinct germination strategies, and species with similar strategies tend to create a homogenous group. Moreover, the study aims to characterise the germination strategies for species groups based on six relevant germination parameters: germination capacity, fresh ungerminated seed, median germination time, germination velocity, germination synchrony, and germination uniformity.

MATERIAL AND METHODS

Diaspore collection. The ripe diaspores (fruits and seeds) were collected in the Mazovian Voivodeship (25–50 km from Warsaw) in central Poland. Fifteen species from the Lower Pilica Valey (PLH 140016; 51°51'N, 21°16'E), three species from the Solec Meadows (PLH 140055; 52°03'N, 21°05'E) and five species from the last location, the unprotected meadows in Tymoteuszew, Jakubów commune (52°15'N, 21°39'E) (Table 1). All diaspores of species were hand-collected from at least 20 individual plants in June or October 2022. After collection, the diaspores were cleaned to remove any internal materials and air-dried at room temperature, approximately 20 °C, for 4–6 months.

Botanical characteristics of species. The study covered 23 plant species from 13 different botanical families. Most species (except for the last four) are diagnostic for extensively used, lowland, semi-natural and rich-species permanent grasslands. Nineteen species belonged to meadow and pasture communities of the *Molinio-Arrhenatheretea* class, including 7 species of *Molinietalia* order and 8 species of *Arrhenatheretalia elatioris* order. Four remaining species belonging to other phytosociological units were also found at the collection sites (Table 1). All tested species were wild (none was a cultivar), and their nomenclature was determined according to Mirek et al. (2020).

Weather conditions. Weather data were recorded from June to September 2022 and mainly focused on at least one month before harvest (Table 2). To understand the environmental effect of seed ripening and germination capacity, the data was also compared to multi-year data from 1981–2010. The average monthly temperatures in 2022 were higher than in the multi-year period, except for September. In terms of precipitation, the monthly precipitation sums were lower compared to the multi-year data, with June and August being very dry (Table 2).

Germination experiment. The germination test was conducted for the 34-day study period at the Botany Department of Warsaw University of Life Sciences from February to March 2023. According to the rules of ISTA (International Seed Testing Association) (2015), the test was carried out in a completely randomised design with three replications of 50 seeds each. These seeds were placed in plastic Petri dishes (diameter 94 mm) on filter paper moistened with distilled water (volume of distilled water 1 – 1.5 mL/Petri dish) tied with parafilm. Water was added to the Petri dishes when they lost up to 60% of their water retention or were dry. All Petri dishes were placed in a versatile environmental test chamber (PHcbi Model No. MLR-352H-PE; Gunma, Japan) for 20 °C/16 h (in the dark) and 30 °C/8 h (in 1 000 lux light intensity or 1 active LED lamp).

The germinated seeds were counted every two days, and any germinated seeds were removed at each counting. The criterion of germination is indicated by a radicle protrusion of ≥ 2 mm. At the end of the research period, the remaining seeds in all Petri dishes were checked and divided into two groups: fresh ungerminated seed (FUS) and dead seed (DS), based on the embryo condition (ISTA 2015). Fresh ungerminated seeds are seeds with a hard seed coat, with the embryo still inside and not infected by fungi or microorganisms, but which do not germinate in a given research period. Dead seeds are seeds with a soft seed coat and loss of viability because the embryo decomposes due to being attacked by fungi or microorganisms.

Germination parameters that were measured:

Germination capacity. Germination capacity (GC) ranges from 0% to 100% and was calculated using the following equation (ISTA 2015):

$$GC = \frac{germinated\ seeds}{total\ number\ of\ seeds} \times 100\%$$

The first time of germination, median germination time, t_{peak}, and total of germination days (TGD). The first time of germination (t_0) is the initial germination time; median germination time or t_{50} is the time at which the number of germinated seeds

https://doi.org/10.17221/46/2025-PSE

Table 1. Botanical characteristics of 23 plant species

Phytosociological units/species	Family	Life cycle[1]	Life form[2]	Seed collection location[3]	Seed harvest time
***Molinio-Arrhenatheretea* (Class)**					
Alopecurus pratensis L.	Poaceae	P	H	1	July
Centaurea jacea L.	Asteraceae	P	H	3	October
Lathyrus pratensis L.	Fabaceae	P	H	2	July
Plantago lanceolata L.	Plantaginaceae	P	H	1	July
***Molinietalia* (Order)**					
Sanguisorba officinalis L.	Rosaceae	P	H	1	October
Silene flos-cuculi (L.) Greuter & Burdet	Caryophyllaceae	P	H	1	July
***Molinion caeruleae* (Alliance)**					
Briza media L.	Poaceae	P	H	3	July
Galium boreale L.	Rubiaceae	P	H	1	October
Succisa pratensis Moench	Caprifoliaceae	P	H	3	October
***Cnidion dubii* (Alliance)**					
Allium angulosum L.	Amarylidaceae	P	G	1	October
Kadenia dubia (Schkuhr) Lavrova & V.N. Tikhom.	Apiaceae	P	H	1	October
***Arrhenatheretalia elatioris* (Order)**					
Achillea millefolium L.	Asteraceae	P	H	1	October
Leucanthemum vulgare Lam.	Asteraceae	P	H	1	July
***Arrhenatherion elatioris* (Alliance)**					
Arrhenatherum elatius (L.) P.Beauv. ex J. Presl & C. Presl	Poaceae	P	H	1	July
Campanula patula L.	Campanulaceae	B, P	H	3	July
Geranium pratense L.	Geraniaceae	P	H	1	October
Knautia arvensis (L.) Coult.	Caprifoliaceae	P	H	3	July
Tragopogon pratensis L.	Asteraceae	B	H	2	July
***Cynosurion* (Alliance)**					
Scorzoneroides autumnalis (L.) Moench	Asteraceae	P	H	2	July
Others					
Dianthus deltoides L.	Caryophyllaceae	P	H	1	July
Eryngium planum L.	Apiaceae	P	H	1	July
Hypericum perforatum L.	Hypericaceae	P	H	1	October
Vicia angustifolia L.	Fabaceae	A	H	1	July

[1]life cycle: A – annual; B – biennial; P – perennial; [2]life form: H – Hemicryptophyte; G – Geophyte; [3]Location of collection: 1 – Lower Pilica Valley; 2 – Solec Meadows; 3 – Tymoteuszew meadow

Table 2. Average temperature and sum of precipitation from June to September 2022 and multi-year (1981–2010)

Year	Average monthly temperature (°C)				
	June	July	August	September	VI–IX
2022	20.2	19.9	22.1	11.6	18.5
1981–2010	16.8	19.0	18.3	13.4	16.9
	The sum of monthly precipitation (mm)				
2022	29.3	103.7	34.4	56.0	223.4
1981–2010	69.8	72.9	62.9	47.3	252.9

VI – June; IX – September. Source: own elaboration based on data recorded at the Meteorological Station of the Warsaw University of Life Sciences

https://doi.org/10.17221/46/2025-PSE

reaches 50% of the total number of germinated seeds; it was calculated using the modification formula of Farooq et al. (2005):

$$t_{50} = T_i + \frac{(\frac{N+1}{2} - N_i)(T_j - T_i)}{N_j - N_i}$$

This is one of the measurements of germination time, where N is the number of finally germinated seeds, and N_i and N_j are the total numbers of seeds germinated in adjacent quantities within a specified time (T_i) and T_j, respectively, when $N_i < \frac{N}{2} < N_j$.

The time shows the peak of species germination during the observation, namely t_{peak}. The formula for t_{peak} was also formulated by Farooq et al. (2005):

$$t_{peak} = \{T_i : N_i = N_{max}\}$$

where: T_i – beginning time of the experiment; N_i – number of germinated seeds in the i^{th} time interval (not the cumulative number); N_{max} – maximum number of germinated seeds in any of the time intervals.

TGD or total germination days means the number of days a species begins and ends its germination period.

Mean germination rate. According to Ranal and Santana (2006), the mean germination rate (MGR) was used to calculate the germination rate for any given time according to the formula:

$$MGR = \frac{\sum_{i=1}^{k} N_i}{\sum_{i=1}^{k} N_i T_i}$$

where: T_i – time from the beginning of the experiment to the i^{th} time interval; N_i – number of seeds germinated in the i^{th} time interval (not the cumulative number, but the number corresponding to the i^{th} time interval); k – total number of time intervals. The MGR value ranges from 0 to 1, with the unit being day.

Timson's index. Timson's index (TI) was used to check the progressive sum of the cumulative germination percentage recorded at specific intervals over a fixed period. The Timson's index formula, according to Khan and Ungar (1984), is as follows:

$$teTI = \sum \frac{G_t}{T}$$

where: G_t – percentage of seeds germinated at time t; T – total germination period. TI is defined in percentage, from 0% to 100% per day.

Germination synchrony and uncertainty. Ranal and Santana (2006) expressed germination synchrony (Z) and uncertainty (U) resulting from germination ata formulated by the following questions:

$$Z = \frac{\sum_{i=1}^{k} C_{N_i,2}}{C_{\sum N_i,2}} \text{, where } \quad C_{N_i,2} = n_i(n_i - 1)/2$$

where: $C_{N_i,2}$ – a combination of seeds germinated at the time i, two together; n_i – number of seeds germinated at that time; N – a partial combination of two germinated seeds out of the total number of seeds germinated in the final count, assuming that all seeds that germinated did so simultaneously. The synchrony index (Z) ranges from 0 to 1. The synchrony index ranges from 0 to 1. Z = 1 when the germination of all the seeds occurs simultaneously, and Z = 0 when at least two seeds can germinate in one at each time. Z can be counted and gives a number if there are only two seeds that complete the seed germination process at the same time. Equals equals:

$$U = \sum_{i=1}^{k} f_i \log_2 f_i \text{, where } f_i = \frac{N_i}{\sum_{i=1}^{k} N_i}$$

where: f_i – relative germination frequency; N_i – number of seeds germinated in i^{th} time; k – final germination time. The uncertainty index (U) was related to the distribution of relative germination frequency. It ranges from $0 \leq U \leq \log_2 n$ with units in bits. Low U values indicate frequencies with a short peak and more concentrated germination over time.

Statistical analysis. The statistical analysis was performed for a dataset covering the results of germination parameters (GC, FUS, DS, t_0, t_{50}, t_{peak}, TGD, TI, MGR, Z, and U) from 23 meadow species. The agglomerative hierarchical clustering method was first performed to establish homogenous groups of the meadow species and was then presented in a dendrogram. Ward's algorithm, using the Euclidean method to calculate the linkage distance for each group, was used in this clustering method. The number of clusters was validated by the Silhouette test. The PCA biplot was used to assess the relationship between relevant parameters and groups of species.

To investigate significant differences between each group's mean rank and interquartile range, the Kruskal-Wallis's and Dunn's tests with Bonferroni correction for six parameters such as GC, FUS, t_{50}, TI, Z and U were performed. Such parameters represented germination performance aspects such as the number of germinated and ungerminated seeds, germination time, velocity, uniformity, and the duration to reach the germination peak, all necessary to develop the germination strategy. The mean rank (*Rm*) represents the average rank assigned to each group within the given parameters, while the interquartile range (IQR) indicates the spread of the data distribution values. The division criteria were determined based on the interquartile range values

https://doi.org/10.17221/46/2025-PSE

from the highest to the lowest for each parameter. Based on IQR, groups are divided into five characteristics of GC and FUS proportions (highest, high, moderate, low, and lowest share). For t_{50}, groups are divided into earliest, early, moderate, late, and latest time to reach t_{50}. TI has five divisions (fastest, fast, moderate, slow, and slowest germination velocity). For the Z and U parameters, each species' characteristics are sorted according to the GC and FUS parameters.

All germination parameters were calculated using the "germination metrics" package (Aravind et al. 2023). A set of the packages "ggplot2", "factoextra" (Kassambra 2020), "tidyverse" and "dplyr" were loaded for clustering and PCA biplot. The Kruskal-Wallis's test and the Dunn's test were performed by "rstatix" (Kassambra 2023) and "rcompanion" (Mangiafico 2025) packages. The results were visualised using "ggplot2" and "ggpubr" packages. All statistical analyses were performed using R Studio 4.4.1 (Boston, USA) and Microsoft Excel (Washington, USA).

RESULTS

The hierarchical clustering of 23 meadow species. Cluster analysis is illustrated in the dendrogram, as shown in Figure 1. Euclidean distance was used to create the dendrogram linkage distances with different cut-off points along the horizontal axis. This clustering method generates five groups marked in Figure 1 with different colours: green (*S. flos-cuculi*, *S. autumnalis*, *L. vulgare*, *A. millefolium*, and *A. pratensis*), purple (*C. jacea*, *A. elatius*, *P. lanceolata*, *D. deltoides*, and *T. pratensis*), orange (*S. pratensis*, *K. dubia*, *H. perforatum*, *S. officinalis*, *A. angulosum*, *E. planum*, *G. boreale*, and *C. patula*), blue (*L. pratensis*, *G. pratense*, and *V. angustifolia*), and red (*K. arvensis* and *B. media*). Some groups with close relationships are marked with a low cut-off point in the dendrogram, such as green, purple and orange groups, while these groups have a high cut-off point, with blue and red groups meaning a distant relationship between these three groups and the remaining two groups.

The PCA biplot of 23 meadow species. The PCA biplot (Figure 2) illustrates the species distribution along two principal components in Dim1 (38.5%) and Dim2 (28.1%), which explained 66.6% of the total variance. The group division on PCA is marked with the same colours and species as the clustering with specific numbers. Group 1 (green) is positioned almost in the middle of the axis but in the positive Dim2 direction with the Z trait. Group 2 (orange) has negative Dim2 values, meaning it has low (below average) values for the Z trait, which correlate positively with Dim2. This group also has above-average values

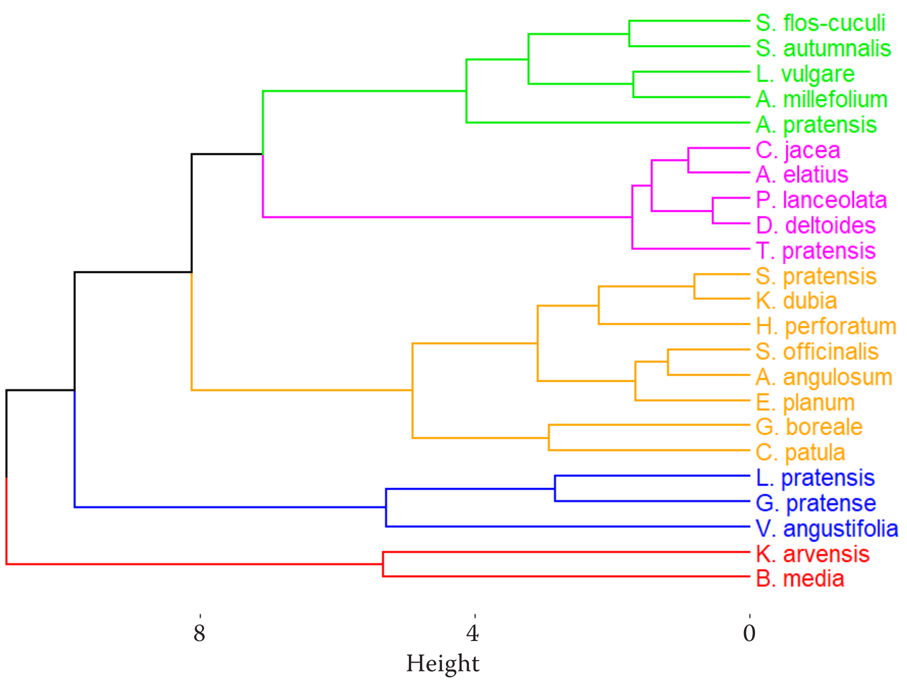

Figure 1. Cluster dendrogram for 23 species classified into different colours. Height (on the *x*-axis) is the distance or dissimilarity value, meaning that the higher the value, the greater the dissimilarity between species in the cluster

https://doi.org/10.17221/46/2025-PSE

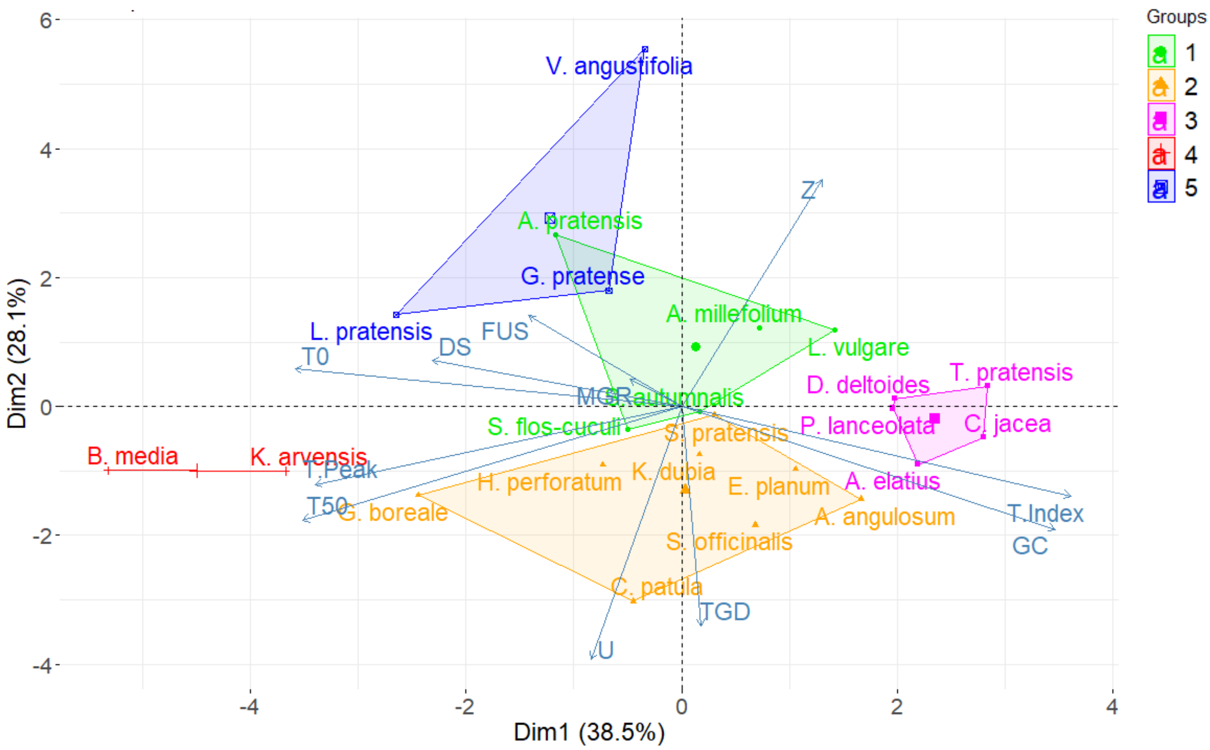

Figure 2. The PCA biplot indicated five distinct groups. GC – germination capacity; t_{50} – median germination time; T index – Timson index; Z – germination synchrony; U – germination uncertainty; t_0 – first germination time; t_{peak} – peak of germination; TGD – total germination days; DS – dead seeds; FUS – fresh ungerminated seeds; MGR – mean germination rate

for traits negatively correlated with Dim2, such as U and TGD. On the other hand, group 3 (purple) is positively aligned along Dim1 in Timson's index and GC, which is opposite to group 4 (red), positioned in extremely negative Dim1 and negative Dim2 for t_{50} and t_{peak} traits, suggesting a long period to reach 50% of the total number of germinated seeds for this group. Group 5 (blue) is negatively correlated with traits in Dim2 such as t_{50}, t_{peak}, and U. Still, it is positioned in the positive Dim1 for FUS, DS, and t_0 traits, indicating that this group is highly associated with a high share of these traits.

Assessment of significant differences among groups. Kruskal-Wallis's analysis demonstrated that there were significant differences between the mean rank and interquartile of the five groups in six parameters (GC, FUS, t_{50}, TI, Z and U) (Table 3). Due to significant differences in all parameters, Dunn's test analysis was performed to compare which specific groups differed significantly from others in the six parameters (Figure 3).

Based on Figure 3A, group 3 (IQR of GC 75–86%) showed the most significant differences in GC compared to other groups, namely group 1 (26–37%), 2 (49.5–70%), 4 (1.8–5.5%), and 5 (4–14%). The comparison of IQR values in group 5 (68–86%) with the other groups differed significantly for the FUS parameter, followed by the difference between groups 2 and 3 (IQR of FUS 19 – 48.5% and 6 – 14%, respectively) (Figure 3B). The high share of FUS from group 5 may indicate a dormant strategy of species from this group. In the t_{50} parameter (Figure 3C), groups 1 (4.4–7.1 days) and 3 (4.4–5.3 days) showed a significant difference compared to groups 2 (8.2–11 days) and 4 (10–22.8 days). This result revealed that groups 1 and 3 required a shorter time to reach half of the total germinated seeds than groups 2 and 4.

Group 3 was reported to have the fastest germination velocity referring to Timson's index IQR range (33–38.1% per day), followed by groups 2 (13–25.8% per day) and 1 (10–16.4% per day) (Figure 3D). The IQR comparison in the Z index between groups 4 (0–0.05) and 5 (0.3–1) revealed the most significant difference. This showed that the occurrence of at least two germinated seeds simultaneously was rare for species from group 5. In the U index, group 5 (IQR 0–1.3 bits) was compared significantly with group 2 (2.2–2.6 bits), suggesting that the frequency of germinated seeds in group 5 oc-

https://doi.org/10.17221/46/2025-PSE

Table 3. The Kruskal-Wallis's tests compare the mean rank (*Rm*) and interquartile range (IQR) of five groups across six parameters

Parameter		Group 1	Group 2	Group 3	Group 4	Group 5	*df*	χ2	*P*-value
GC (%)	*Rm*	24.73	40.97	60.5	7.83	12.28	4	52.78	< 0.0001*
	IQR	26–37	49.5–70	75–86	1.8–5.5	4–14			
FUS (%)	*Rm*	26.87	41.04	21.07	21.67	64.56	4	34.15	< 0.0001*
	IQR	4–17	19–48.5	6–14	4.5–19.5	68–86			
t_{50} (days)	*Rm*	23.07	49.23	16.07	57.92	33.22	4	38.66	< 0.0001*
	IQR	4.4–7.1	8.2–11	4.4–5.3	10–22.8	5–8			
TI (% per day)	*Rm*	27.1	39.15	60.83	6.5	13.06	4	51.1	< 0.0001*
	IQR	10–16.4	13–25.8	33–38.1	0.8–1.5	1.7–4.4			
Z	*Rm*	42.8	28.08	41.87	6.33	48.11	4	23.05	0.00012*
	IQR	0.2–0.47	0.17–0.25	0.2–0.3	0–0.05	0.3–1			
U (bits)	*Rm*	24.97	53.29	36.5	18.92	11.17	4	40.44	< 0.0001*
	IQR	0.7–1.95	2.2–2.6	1.8–2.1	0.3–1.8	0–1.3			

GC – germination capacity; FUS – fresh ungerminated seeds; t_{50} – median germination time; TI – Timson's index; Z – germination synchrony; U – germination uncertainty; *Rm* – mean rank; IQR – interquartile range; *df* – degrees of freedom; χ2 – chi-square value; *P*-value – probability value; *$P < 0.05$

curred in a shorter peak than in group 2. Meanwhile, pairwise comparisons of the IQR between group 1 and other groups, such as groups 3, 4, and 5, showed non-significant differences (Figure 3F).

From the results of the Kruskal-Wallis and Dunn's tests, all groups are ordered based on IQR from the highest to the lowest value to determine the specific germination strategies for the six parameters (Table 4). For the Z index, a higher IQR value means more synchronous germination and *vice versa*. In contrast, in the U index, a higher IQR value indicates a longer period to reach peak germination and *vice versa*.

DISCUSSION

In our study, we distinguished five groups of germination strategies within the meadow species occurring in *Arrhenatherion* meadows in central Poland. Germination strategies varied depending on each group's germination performances of six selected

Table 4. Germination strategies of five groups based on interquartile range (IQR) value order

Parameter	Group 1	Group 2	Group 3	Group 4	Group 5
GC (%)	20–49 (moderate)	49.5–70 (high)	75–86 (the highest)	1.8–5.5 (the lowest)	4.0–14 (low)
FUS (%)	4.0–17 (low)	19–48.5 (high)	6.0–14 (the lowest)	4.5–19.5 (moderate)	68–86 (the highest)
t_{50} (days)	4.4–7.1 (early)	8.2–11 (late)	4.4–5.3 (the earliest)	10–22.8 (the latest)	5–8 (moderate)
TI (% per day)	10–16.4 (moderate)	13–25.8 (fast)	33–38.1 (the fastest)	0.8–1.5 (the slowest)	1.7–4.4 (slow)
Z	0.2–0.47 (high)	0.17–0.25 (low)	0.2–0.3 (moderate)	0–0.05 (the lowest)	0.3–1 (the highest)
U (bits)	0.7–1.95 (moderate)	2.2–2.6 (the highest)	1.8–2.1 (high)	0.3–1.8 (low)	0–1.3 (the lowest)

GC – germination capacity; FUS – fresh ungerminated seeds; t_{50} – median germination time; TI – Timson's index; Z – germination synchrony; U – germination uncertainty

https://doi.org/10.17221/46/2025-PSE

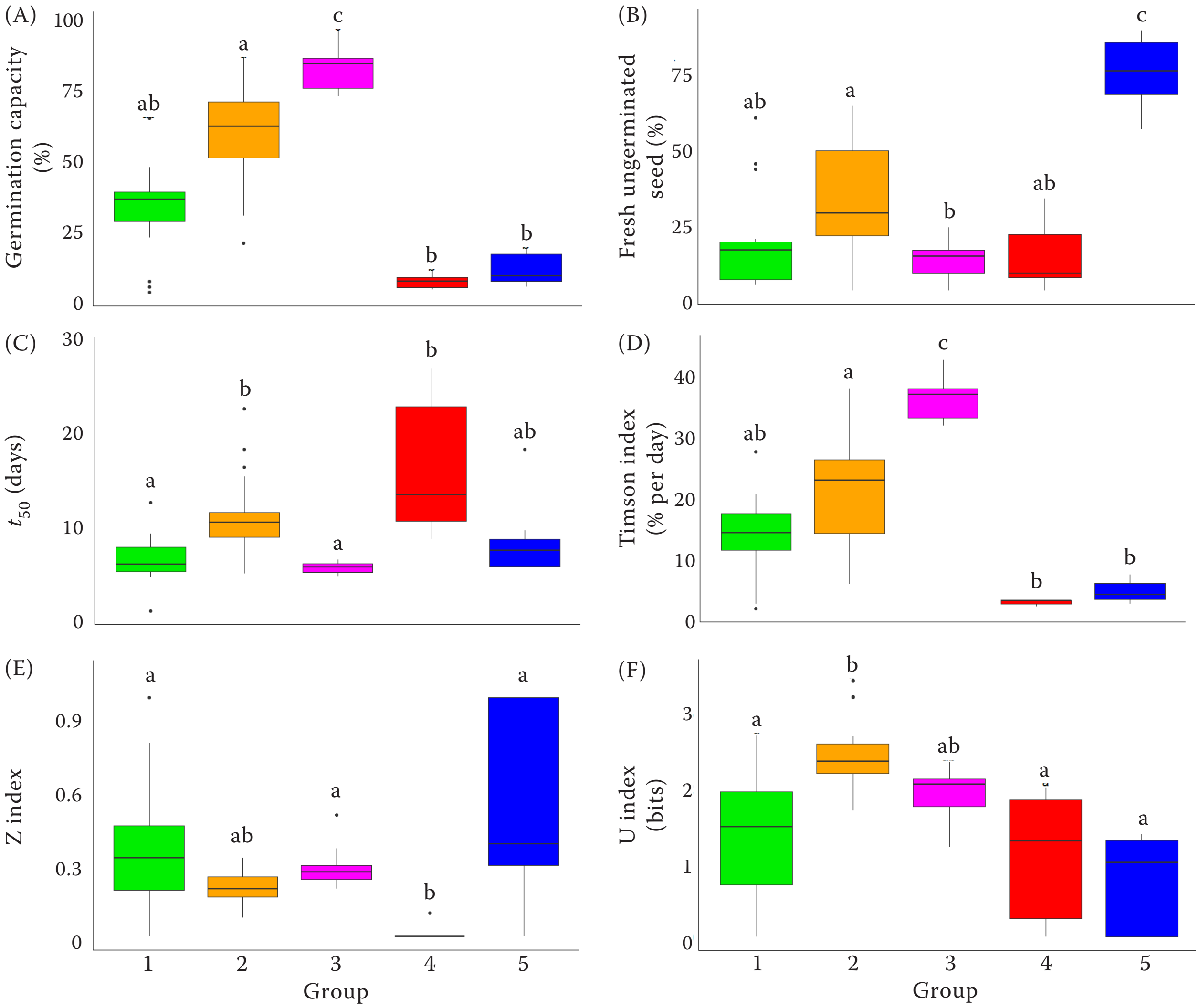

Figure 3. Boxplot of the Dunn's test: (A) germination capacity; (B) fresh ungerminated seed; (C) median germination time (t_{50}); (D) Timson index; (E) germination synchrony (Z); (F) germination uncertainty (U). The same letters indicate a non-significant difference in $P < 0.05$

parameters. In terms of GC, FUS, t_{50}, TI, Z and U, those parameters enabled the diversity of germination strategies to be defined, which agreed with the findings of Zhang et al. (2021) and Zhao et al. (2021). They found that assessing germination capacity (%), germination timing aspects and seed dormancy described the division of germination strategies in grassland species due to the diversity of specific species' germination responses to light availability. Considering the aspects of germination timing and germination uniformity can also determine the clear variability in the time of species co-existence at the plant community level (Bu et al. 2008).

The highest germination capacity, combined with the fastest germination velocity of group 3 species, such as *P. lanceolata*, *T. pratensis*, and *A. elatius*, also recorded the same results as the study by Scotton (2016), which showed that these species have high adaptability and germinabilities, dominating about 92% of the restored *Arrhenatherion* meadow area in Italy for four years. These high germination performances indicate the concordance of the source climate during seed maturation and the temperature in the experiment so that the adverse maternal effect on the seeds may disappear (Veselá et al. 2020). Group 2 species, collected mainly in October, showed high germination capacity but a longer period to reach the t_{50} point. These germination performances may result in the effect of the source climate at collection to delay the activation of germination signals due to the incompatibility of light availability until the next growing season to ensure plant establishment (Seglias et al. 2018).

https://doi.org/10.17221/46/2025-PSE

Our results are also in agreement with previous studies by Löfgren (2002) and Picó and Koubek (2003), mainly for two *Asteraceae* species from group 1 (*A. millefolium* and *S. autumnalis* – the previous name was *Leontodon autumnalis*), which showed that inbreeding and high levels of self-incompatibility can reduce germination capacity by producing non-viable seeds in the maternal plants. At the same time, other species in this group required more information but were not explored further in this study. Meanwhile, the thick layer of the seed coat of species from *Fabaceae* and *Geraniaceae* families from group 5 caused a morphological limitation of the imbibition time, which had a direct impact on the low GC and high FUS proportion (Janicka et al. 2021). The extended imbibition period in dormant species contributes to the high germination synchrony, as germination reaches the peak in a shorter time than in non-dormant species (Zhang et al. 2021), as reflected by the low U index of group 5.

This study also found that two species (*K. arvensis* and *B. media*) had the lowest GC proportion and the latest time to reach t_{50}, corresponding to the slowest germination velocity. These lowest germination results can probably be explained by the presence of physiological dormancy found in *K. arvensis* (Vange et al. 2004), in which this type of dormancy reduced the germination capacity of the species by up to 71% (Zhao et al. 2021). On the other hand, native grass species such as *B. media* are weak competitors and tend to germinate at an optimal temperature of around 15 °C after a month of dry storage (Jensen 2004). Therefore, this species' specific temperature and storage time requirements were probably not met in our study, which could have contributed to its reduced germination performances.

Global demand for local species for restoration is likely to increase, which should coincide with the knowledge of the diversity of germination strategies based on germination performances (Pedrini et al. 2020). For this reason, to mitigate nature's self-renewal process, sowing species with rapid germination and survival at high density in the first year is strongly recommended because it ensures the coverage of species introduced in restored areas (Scotton 2016). Species such as *A. elatius*, *C. jacea*, *P. lanceolata*, *T. pratensis* and *D. deltoides* can help maintain plants in the sward by rapidly developing rosette leaves. Information on the germination strategy of dormant species and species with low germination performances can also help ecological experts to decide on the pre-germination treatments before sowing (i.e. GA3 or KNO_3 treatment) or to determine the seed mixture proportion of species with those strategies and suitable sowing date (Kildisheva et al. 2020).

To sum up, germination performance refers to germination capacity, the proportion of fresh ungerminated seeds, median germination time, Timson's index, germination synchrony, and germination uncertainty, allowing diverse germination strategies for meadow species. Moreover, species exhibiting high germination performances are considered the most suitable for introduction to direct drilling, notably to support successful establishment at the initial stage of ecological restoration. Future research on the germination strategies of meadow species is necessary to optimise seed proportions in mixtures.

Acknowledgement. We thank Dr. Mirosław Sobczak (Head of the Botany Department, Warsaw University of Life Sciences) for his valuable support and permission to use the versatile environmental test chamber during the experiment. We also thank Dr. Marcin Studnicki (Biometric Department, Warsaw University of Life Sciences) for his valuable help in correcting our result interpretation and consulting statistical analysis.

REFERENCES

Aravind J., Devi S.K., Radhmani J., Jacob S.R., Srinivasan K. (2023): Germinationmetrics: Seed Germination Indices and Curve Fitting (Version 0.1.8) [R package]. GitHub & CRAN. Available at: https://CRAN.R-project.org/package=germinationmetrics

Bu H., Du G., Chen X., Xu X., Liu K., Wen S. (2008): Community-wide germination strategies in an alpine meadow on the eastern Qinghai-Tibet plateau: phylogenetic and life-history correlates. Plant Ecology, 195: 87–98.

European Commission (2021): EU Biodiversity Strategy for 2030: Bringing Nature Back into our Lives. Luxembourg, Publication Office of the European Union, 1–35.

Farooq M., Basra S.M.A., Ahmad N., Hafeez K. (2005): Thermal hardening: a new seed vigor enhancement tool in rice. Journal of Integrative Plant Biology, 47: 187–193.

Hay F.R., Probert R.J. (2013): Advances in seed conservation of wild plant species: a review of recent research. Conservation Physiology, 1: 1–11.

ISTA (2015): Chapter 5: The germination test. In: International Rules for Seed Testing. Zurich, International Seed Testing Association, 5–56.

Janicka M., Pawluśkiewicz B., Małuszyńska E., Gnatowski T. (2021): Diversity of the seed material of selected plant species of naturally valuable grassland habitats in terms of the prognosis of introduction success. Sustainability, 13: 13979.

Jensen K. (2004): Dormancy patterns, germination ecology, and seed-bank types of twenty temperate fen grassland species. Wetlands, 1: 152–166.

Kassambara A. (2020): Factoextra: Extract and visualize the results of multivariate data analyses (Version 1.0.7) [R package]. The Comprehensive R Archive Network. Available at: https://cran.r-project.org/web/packages/factoextra/factoextra.pdf

Kassambra A. (2023): rstatix: Pipe-Friendly Framework for Basic Statistical Tests (Version 0.7.2) [R package]. The Comprehensive R Archive Network. Available at: https://CRAN.R-project.org/package=rstatix

Khan M.A., Ungar I.A. (1984): The effect of salinity and temperature on the germination of polymorphic seeds and growth of *Atriplex triangularis* Willd. American Journal of Botany, 71: 481–489.

Kildisheva O.A., Dixon K.W., Silveira F.A.O., Chapman T., Di Sacco A., Mondoni A., Turner S.R., Cross A.T. (2020): Dormancy and germination: making every seed count in restoration. Restoration Ecology, 28: 256–265.

Löfgren A. (2002): Effects of isolation on distribution, fecundity, and survival in the self-incompatible *Achillea millefolium* (L.). Ècoscience, 9: 503–508.

Mangiafico S.S. (2025): rcompanion: Functions to support extension education program evaluation (version 2.5.0) [R package]. CRAN. Available at: https://CRAN.R-project.org/package=rcompanion

Mirek Z., Piękoś-Mirkowa H., Zając A., Zając M. (2020): Vascular Plants of Poland. An Annotated Checklist. 3rd Edition. Cracow, W. Szafer Institute of Botany, Polish Academy of Sciences.

Nonogaki H., Bassel G.W., Bewley J.D. (2010): Germination-still a mystery. Plant Science, 179: 574–581.

Pedrini S., Gibson-Roy P., Trivedi C., Gálvez-Ramírez C., Hardwick K., Shaw N., Frischie S., Laverack G., Dixon K. (2020): Collection and production of native seeds for ecological restoration. Restoration Ecology, 28: 228–238.

Picó F.X., Koubek K. (2003): Inbreeding effects on fitness traits in the heterocarpic herb *Leontodon autumnalis* L. (Asteraceae). Acta Oecologica, 24: 289–294.

Ranal M.A., Santana D.G. (2006): How and why to measure the germination process. Revista Brasileira de Botanica, 29: 1–11.

Seglias A.E., Williams E., Bilge A., Kramet A.T. (2018): Phylogeny and source climate impact seed dormancy and germination of restoration-relevant forb species. Plos One, 13: e0191931.

Scotton M. (2016): Establishing a semi-natural grassland: effects of harvesting time and sowing density on species composition and structure of a restored *Arrhenatherium elatius* meadow. Agriculture, Ecosystems and Environment, 220: 35–44.

Vange V., Heuch I., Vandvik V. (2004): Do seed mass and family affect germination and juvenile performance in *Knautia arvensis*? A study using failure-time methods. Acta Oecologica, 25: 169–178.

Veselá A., Dostálek T., Rokaya M.B., Münzbergova Z. (2020): Seed mass and plant home site environment interact to determine alpine species germination patterns along an elevation gradient. Alpine Botany, 130: 101–113.

Zhang C., Willis C.G., Donohue K., Ma Z., Du G. (2021): Effects of environment, life-history and phylogeny on germination strategy of 789 angiosperms species on the eastern Tibetan Plateau. Ecological Indicators, 129: 107974.

Zhao M., Liu Z., Zhang H., Wang Y., Yan W. (2021): Germination characteristics is more associated with phylogeny-related traits of species in a salinized grassland of Northeastern China. Frontiers in Ecology and Evolution, 9: 748038.

Received: February 6, 2025
Accepted: April 22, 2025
Published online: May 29, 2025