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Predicting plant establishment: Germination responses of five *Arrhenatherion* alliance species from two distinct climatic origins

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Highlights
- Enrichment of many lowland hay meadows with native plant species is necessary.
- Species-related and weather factors during seed ripening determine germination efficiency.
- Seedling establishment model can be predicted using a variable seed mass approach.

Abstract: The lowland hay meadows conservation status is increasingly at risk due to improper management and climate change, threatening plant communities, including *Arrhenatherion* alliance. As a result, species enrichment is required. However, natural plant self-establishment remains challenging due to the high variability in germination, largely caused by climate factors. Thus, a germination test is suggested before directly sowing local seeds in the field. Therefore, this study aimed to investigate how germination characteristics of five local species are affected by the interplay between species and weather factors, specifically mean temperature and total rainfall during seed filling and ripening. During warm, dry periods, the seed mass of *Campanula patula* L. and *Centaurea jacea* L. was higher (0.04 g and 1.87 g, respectively), whereas in wet periods, the seed mass of *Achillea millefolium* L. (0.10 g), *Plantago lanceolata* L. (1.24 g), and *Tragopogon pratensis* L. (7.41 g) was higher. The germination capacity was significantly affected by species-specific factors. Seeds of *A. millefolium* and *T. pratensis* during wetter years showed higher germination rates than other species, which exhibited the opposite trend. Additionally, a wetter collection period shortened t_{50} (time required for 50% germination) in all species except *A. millefolium* and *T. pratensis*, while *C. patula* remained unaffected in both years. A positive correlation was observed between seed mass, germination capacity, and speed, while a negative correlation with t_{50}. Hence, an increase in seed mass leads to a reduced t_{50} duration. According to our findings, seed mass may serve as a reliable predictor of plant establishment in the field.

Keywords: climate change, establishment, germination, lowland hay meadow, seed mass

INTRODUCTION

Lowland hay meadows (habitat code: 6510) are one of species-rich semi-natural grasslands protected under the Natura 2000 framework (Council Directive, 1992). However, they face significant threats, including land use changes (such as conversion to arable land, overseeding, and intensive use), abandonment, and climate change (Schils *et al.*, 2022). As a result, from 2013 to 2018, many European countries, including Poland, reported an unfavourable conservation status (EEA, 2019).

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Additionally, fluctuating climatic regimes have resulted in sward degradation, restricting the provision of crucial ecosystem services and limiting the natural self-establish of native species (Jäger *et al.*, 2020). Therefore, the EU biodiversity target for 2021–2030 has been refined, emphasizing the need for more specific research on the ability of local native species to thrive in previously degraded areas to restore biodiversity (Janicka, Pawluśkiewicz and Gnatowski, 2023).

However, because of significant variations in germination capacity and harsh climatic conditions, relying on natural self-establishment of plants remains challenging. Seed germination is a complex process influenced by factors, such as species-specific genetic and environmental factors (Fenner and Thompson, 2005). Therefore, germination capacity should be assessed before sowing (Hölzel and Otte, 2004). For this reason, more wild species exhibit a wide range of environmental requirements to germinate, such as local precipitation, temperature, humidity, and water potential (Rosbakh *et al.*, 2022). Despite this, these species often inherit maternal environmental effects to their progenies so that result in seed dormancy and affected seedling survival (Dalgleish, Koons and Adler, 2010). Such persistent effects may affect the establishment model and prediction of vegetation re-establishment (Kiss *et al.*, 2018).

Although seed mass is often considered the best predictor of germination (Seguí, Jimenez, and Cursach, 2021), a study by Fernández-Pascual *et al.* (2022) shows that seed mass could be a germination predictor for establishment only in certain plants from *Poaceae, Asteraceae,* and *Apiaceae* families. Additionally, germination is reinforced by various environmental factors, such as rainfall, temperature, and soil moisture (Dudney *et al.*, 2017). Consequently, the impact of seed mass as a seed trait is more pronounced in seeds with rapid germination, playing a dominant role in regulating vegetation shifts. The interaction between seed traits and environmental conditions facilitates the development of germination strategies, including an increased proportions of hard seeds and bet-hedging strategies, even among species within similar taxa under unfavourable climatic conditions (Dukes *et al.*, 2011; Xu and Du, 2023).

Previous studies on seed recruitment in grassland plants have primarily focused on seedling numbers and their association with seed mass, often overlooking key aspects of germination quality under distinct climatic regimes. Therefore, this study tries to achieve three aims: (1) investigate the effects of recruitment year and species-specific germination traits, (2) assess the correlation between seed mass and germination characteristics, and (3) develop a regression model to predict the rate of emergence.

MATERIALS AND METHODS

STUDY LOCATION AND WEATHER CONDITION

Diaspores (referred to as seeds) were collected by hand in July and October during two different periods: 2017 and 2022. The collection took place in a Special Habitat Protection Area – the Lower Pilica Valley (Dolina Dolnej Pilicy; Polish Habitat Code: PLH 140016), near the Mniszew Town (51°50'04.1"N 21° 15'57.2"E, 51°50'00.3"N 21°17'05.2"E). The collected diaspores belonged to five selected species characteristic of lowland hay meadow (6510) such as *Achillea millefolium* L., *Campanula patula* L., *Centaurea jacea* L., *Plantago lanceolata* L., and *Tragopogon pratensis* L.

The two collection years, 2017 and 2022, represented different growing seasons with varying weather conditions. Daily precipitation and temperature were monitored during the seed ripening period, i.e. from June to September (Tab. 1). Then, the hydrothermal index of Vinczeffy (1984) was calculated as quotient of total precipitation and total temperature. This index was used to classify the two sourcing years. Vinczeffy (1984) describes the hydrothermal index as follows: rainy (>0.2), wet (0.175–0.199), medium moist (0.150–0.174), dry (0.125–0.149), very dry (0.1–0.124), extremely dry (<0.1). As a result, the 2017 and 2022 growing seasons (from April to September) were classified as wet (0.194 mm·(°C^{-1})) and dry (0.111 mm·(°C^{-1})), respectively. In 2017, total monthly precipitation was greater than multi-year data, while in 2022, they were lower, especially June and August were very dry compared to multi-year data. With respect to air temperature, average monthly temperatures in both 2017 and 2022 were higher than in the multi-year average, except for September 2022.

Table 1. Mean monthly temperature (°C) and total of monthly precipitation (mm) during the seed ripening of selected plant species in 2017 and 2022

Year	Value in				
	Jun	**Jul**	**Aug**	**Sep**	**Jun–Sep**
Average monthly temperature (°C)					
2017	18.9	19.2	20.1	14.1	18.1
2022	20.2	19.9	22.1	11.6	18.5
1981–2010	16.8	19.0	18.3	13.4	16.9
Sum of monthly precipitation (mm)					
2017	106.2	111.0	68.5	146.8	432.5
2022	29.3	103.7	34.4	56.0	223.4
1981–2010	69.8	72.9	62.9	47.3	252.9

Source: own elaboration based on data recorded at the Meteorological Station of the Warsaw University of Life Sciences (WULS-SGGW).

BOTANICAL CHARACTERISTICS OF FIVE SPECIES

The research covered five plant species commonly found in extensively managed lowland hay meadows (code 6510; All. *Arrhenatherion elatioris*) – Table 2. Most of them are perennials. All species are hemicryptophytes, meaning they have renewal buds at ground level, protected by a layer of leaf litter and soil. Three species spread by single-seeded fruit (non-bursting).

GERMINATION TEST

Before conducting the germination test, pure seeds were separated from inert matter by laboratory sieves and weighed on a digital analytical balance (accuracy of 0.00001 g). To determine the thousand seed mass (*TSM*), 100 seeds were weighed in four replications. The seeds were then placed in plastic Petri dishes (90 mm in diameter) lined with moistened

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Table 2. Botanical characteristics of five species of Lowland Hay Meadows (6510)

No.	Species	Family	Plant life cycle	Plant life form	Type of diaspore
1	*Achillea millefolium* L.	*Asteraceae*	P	H	fruit
2	*Campanula patula* L.	*Campanulaceae*	B, P	H	seed
3	*Centaurea jacea* L.	*Asteraceae*	P	H	fruit
4	*Plantago lanceolata* L.	*Plantaginaceae*	P	H	seed
5	*Tragopogon pratensis* L.	*Asteraceae*	B	H	fruit

Explanations: B = biennial, P = perennial, H = hemicryptophyte.
Source: own elaboration on the basis of nomenclature of species according to Mirek *et al.* (2020); life form using the Raunkiaer scale, acc. to Ellenberg and Leuschner (2010); diaspore – acc. to Cappers, Bekker and Jans (2006).

filter paper. The filter paper was hydrated with distilled water (2 cm^3 every two days, if dried) and sealed with parafilm to prevent water loss. According to ISTA (2018) rules, Petri dishes were placed in a versatile-environment chamber and subjected to a photoperiod regime of 20°C for 16 h in darkness and 30°C for 8 h under 1000 lx LED lamp.

The germination test was performed to evaluate germination attributes, such as germination capacity (*GC*, in % with respect to normal seedlings), abnormal seedling (*AS*), dead seeds (*DS*), fresh-ungerminated seeds (*FS*), median germination time (t_{50}), and germination velocity (*GV*). The germination criteria followed ISTA (2018) standards, where a protruding radicle ≥2 mm long of seed indicated a germinating seed or seedling. For very small seeds (e.g. *C. patula*), germination was observed under a magnifying glass. Seedlings were then counted every two days for 34 days and analysed to distinguish between normal or abnormal seedlings. After 34 days of the germination test, the viability of the remaining seeds was examined to differentiate dead seeds from fresh-ungerminated ones.

PARAMETERS OF GERMINATION

- **Germination capacity**

Germination capacity (*GC*) is defined as the percentage of total number of normally germinating seeds in given experimental period. It was calculated according to the Equation (1):

$$\%GC = \frac{total\ number\ of\ normally\ germinating\ seeds}{total\ seeds}\ 100\% \quad (1)$$

- **Abnormal seedlings**

According to the ISTA (2018), an abnormal seedling can be classified according to several defects: (1) damaged seedlings, (2) deformed seedlings, and (3) decayed seedlings.

- **Dead seeds and fresh-ungerminated seeds**

Dead seeds are seeds that failed to germinate by the end of the experiment. They are neither fresh nor hard and cannot produce cotyledon or any part of the seedling. When pressed at the end of the experiment, they appear collapsed, often releasing a milky paste.

Meanwhile, fresh-ungerminated seeds do not germinate but remain firm, clean, and seemingly viable. Unlike hard seeds, they do not exhibit dormancy. At the end of the germination test, their coat remains intact (ISTA, 2018).

- **Median germination time (t_{50})**

Median germination time or t_{50} describes the time to reach 50% of maximum germination (germination capacity or defined as the total number of normal seedlings). Equation (2) was designed by Farooq *et al.* (2005):

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

where: N = final number of germinated seeds, and N_i and N_j = total number of germinated seeds in adjacent counts (days) at times T_i and T_j assuming that $N_i < \frac{N}{2} < N_j$.

- **Germination velocity**

Timson index is used to calculate the germination velocity (rate) according to the Equation (3) (Timson, 1965):

$$GV = \frac{\sum G}{t} \quad (3)$$

where: G = percentage of seed germination at a 2-day interval, t = total germination period; a higher value of G indicates a faster germination rate.

STATISTICAL ANALYSIS

All data were assessed using a two-way analysis of variance (ANOVA). Two factors were analysed for all parameters: the species factor and recruitment year (2017 and 2022), representing two different growing seasons. To improve data normality, values for abnormal seedlings, dead seeds, and fresh-ungerminated seeds were arcsine transformed before conducting the two-way ANOVA. Then, statistically significant results of the ANOVA were analysed using a *LSD* post-hoc Tukey test with a 95% confidence level.

Pearson correlation was used to assess the relationship between seed mass and three important parameters (germination capacity, germination velocity, and t_{50}) in 2017 and 2022. Additionally, linear regression was also established between t_{50} and seed mass. The equation was split over two years (2017 and 2022). All statistical analyses were performed using R studio (version 4.3.0).

RESULTS AND DISCUSSION

EFFECT OF SPECIES AND MATERNAL ENVIRONMENT ON SEED TRAITS AND GERMINATION

A two-way ANOVA analysis showed that the species-specific factor with two different climatic regimes and their interaction had significant effect on most parameters, except for abnormal seedlings and t_{50} (Tab. 3).

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Table 3. Two-way ANOVA parameters related to the effects of two different climatic regimes to selected species, and their interactions on seed mass and germination attributes

Para-meter	Species (A)		Climate regime (B)		A × B		Error
	d.f.	*F*-ratio	*d.f.*	*F*-ratio	*d.f.*	*F*-ratio	*d.f.*
TSM	4	2,014.35*	1	1.78 ns	4	9.51*	20
GC	4	135.21*	1	10.60*	4	72.78*	20
AS	4	0.93 ns	1	3.87 ns	4	0.93 ns	20
DS	4	27.23*	1	0.50 ns	4	18.52*	20
FS	4	144.84*	1	13.64*	4	43.64*	20
t_{50}	4	21.04*	1	7.08*	4	2.68 ns	20
GV	4	150.37*	1	28.90*	4	40.18*	20

Explanations: *TSM* = thousand seed mass, *GC* = germination capacity, *AS* = abnormal seedlings, *DS* = dead seeds, *FS* = fresh-ungerminated seeds, t_{50} = median germination time, *GV* = germination velocity, *d.f.* = degree of freedom, ns = non-significant at $p > 0.05$ in $\alpha = 0.05$, * = significant at $p < 0.05$ in $\alpha = 0.05$.
Source: own study.

The observation of seed mass showed that *T. pratensis* and *C. jacea* exhibited the highest difference of TSW in both years (Fig. 1a). While *T. pratensis* seed mass decreased by more than 0.35 g in 2022, *C. jacea* seeds responded by increasing by 0.2 g during dry period. Moreover, both species expressed the most contrasting response among all species from *Asteraceae* family – *A. millefolium* which was more stable in terms of seed mass in wet and dry growing seasons.

This response can be considered part of the intraspecific variability, in line with Murray *et al.* (2004) who examined seed mass variability of *Glycine* species within a similar family. Contrary to the findings of Janicka *et al.* (2021), which reported that rising temperatures accompanied by decreasing precipitation led to reduced seed mass and size, the present study did not find a significant impact of environmental conditions on seed mass reduction. Nevertheless, the phylogenetic role may influence seed mass decline during drought periods, as reported by Xu and Du (2023). Future research should examine the influence of that role on the germination behaviour of species from *Arrhenatherion* communities under varying climatic conditions, as this aspect was not observed in the present study.

Declining precipitation combined with rising temperatures in 2022 had varying effects on germination capacity. Three species: *C. patula, C. jacea,* and *P. lanceolata* – responded positively in terms of germination capacity when collected in the dry period as opposed to the wet period, while the remaining two species showed a decline in the number of germinating seeds (Fig. 1b). Regarding *A. millefolium*, seed germination capacity in 2022 was more than twice as low as in 2017 (approx. 35%) – Figure 1a. This finding partly aligns with the results of Fry, Manning, and Power (2014), who highlighted that germination responses of forbs are better adapted to anticipating rare rainfall events during prior dry periods compared to non-legume forbs. Presumably, these differences in germination capacity reflect survival strategies in response to climatic variability (Fay and Schultz, 2009).

In both climatic regimes, species responses varied in terms of dead seeds (*DS*) and fresh-ungerminated seeds (*FS*). Seeds collected during the wet period of 2017 included more dead seeds than those collected during the drier and warmer period, except for *T. pratensis* (Fig. 2a). Conversely, all species survived the period of drier growth and produced increased quantity of *FS* (Fig. 2b). Seed size and micro-climate conditions during seed harvesting were considered key factors in determining the threshold of germination, influencing the timing of germination signals and seed dormancy breaking (Veselá *et al.*, 2020). Despite this, the presence of *FS* indicated a lower competitive ability for specific species. These species can be classified as specialists, which may imply sowing strategies related to germination shifts (Kövendi-Jakó *et al.*, 2017).

We found that in 2017 two species had the shortest t_{50}: *P. lanceolata* (2.62 days) and *C. jacea* (2.82 days). In 2022, *A. millefolium* (3.81 d) had the shortest t_{50}. However, the longest t_{50} period was recorded for the smallest seeds of *C. patula* in both years (9.14 d in 2017 and 15.58 d in 2022) – Figure 3a. This reflected a slow germination velocity for this species of approximately 1.28 germinating seeds per day in 2017 and 1.18 germinating seeds per day in 2022 (Fig. 3b).

Improper light and temperature conditions during the experiment inhibited carbohydrate breakdown which decreased the amount of energy available for seed emergence, as observed in *C. patula* (Koutsovoulou, Daws and Thanos, 2014). Nonetheless, with intermittent rainfall, smaller seeds benefited from larger seeds by delaying germination to approximately 60 days longer than

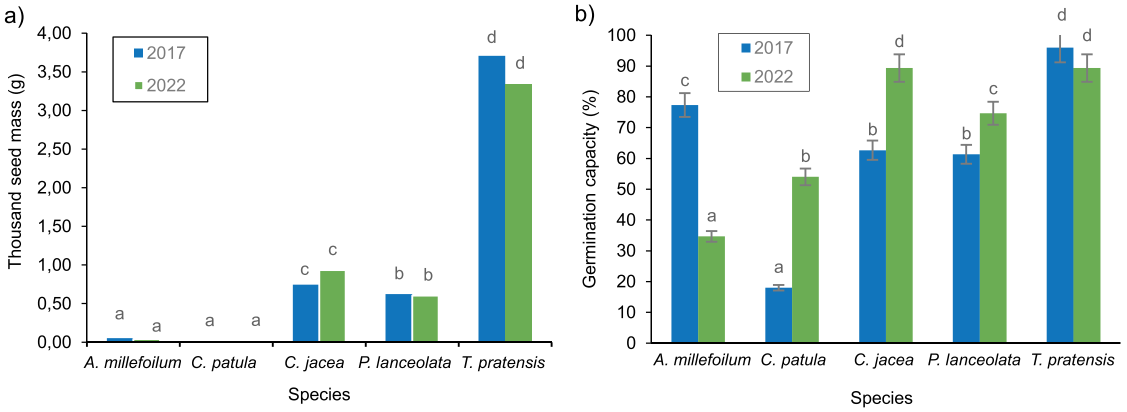

Fig. 1. The effect of two distinct climatic regimes in 2017 and 2022 on five selected species in relation to: a) thousand seed mass, b) germination capacity; source: own study

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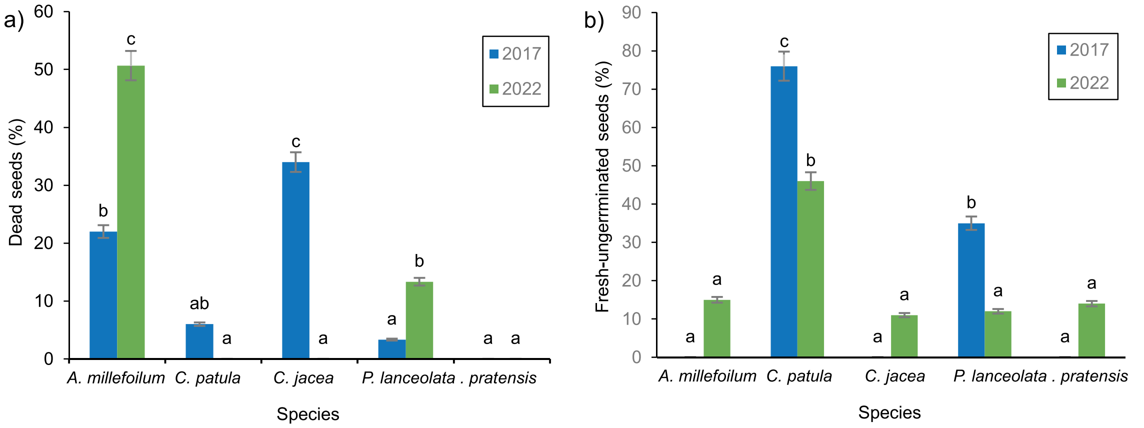

Fig. 2. The effect of two distinct climatic regimes in 2017 and 2022 on five selected species with respect to: a) dead seeds, b) fresh-ungerminated seeds; source: own study

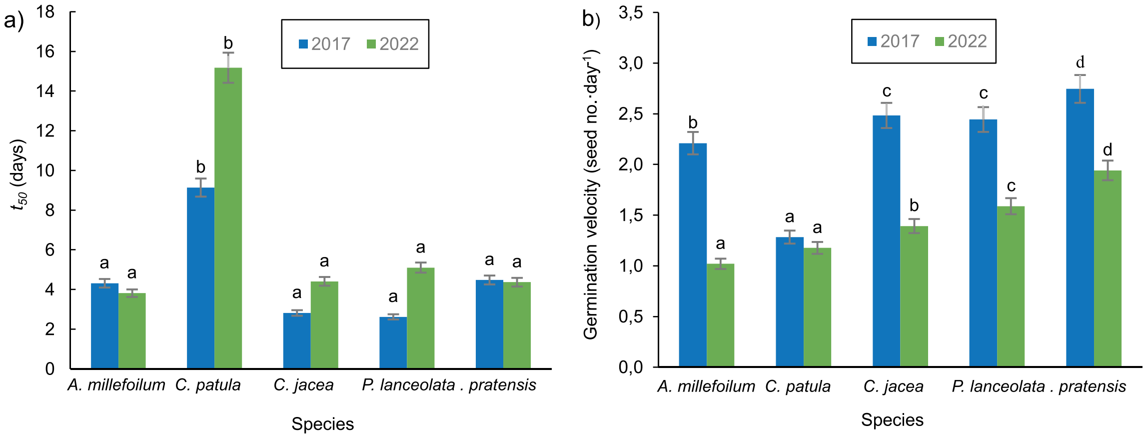

Fig. 3. The effect of two distinct climatic regimes in 2017 and 2022 on five selected species with respect to: a) median germination time (t_{50}), b) germination velocity (seed no.·d^{-1}). The same letters indicate a non-significant difference according to the *LSD* post-hoc test (p < 0.05 in α = 0.05); source: own study

larger seeds (O'Brien *et al.*, 2013). As a result, this mechanism may help maintain their ecological niche and contribute to species richness within the sward (Donohue *et al.*, 2010). Understanding this mechanism is necessary to decide the appropriate proportion of different seed fractions in seed mixtures.

CORRELATION BETWEEN SEED MASS, GERMINATION CAPACITY, GERMINATION VELOCITY AND MEDIAN GERMINATION TIME

Pearson correlation was performed for all parameters in 2017 and 2022. Then, strong positive correlations were found between *TSM* and *GC* and *GV*. However, *TSM* was negatively correlated with t_{50} (Tab. 4).

This study demonstrated that an increase in seed mass among the tested species was associated with a reduction in t_{50}, supporting the assumption that heavier seeds may accelerate germination velocity. Wang *et al.* (2018), and Yi *et al.* (2019) reported similar findings, indicating that species with larger seed volumes can shorten the emergence timing by optimising their high nutrient content in the cotyledon. This accelerates the germination rate and produces a greater number of germinated seeds compared to lighter seeds. These correlation values revealed that seed traits may serve as crucial predictors of plant establishment.

Table 4. Pearson correlation table for the relationship between seed mass (*TSM*), germination capacity (*GC*), germination velocity (*GV*) and median germination time (t_{50}) for 2017 and 2022

Parameter	*TSM*	
	2017	**2022**
TSM	1	1
GC	0.679	0.695
GV	0.634	0.685
t_{50}	–0.202	–0.343

Explanations: Pearson correlation value from –1 to 1 which means –1 is strong negative correlation, and 1 is strong positive correlation.
Source: own study.

LINEAR REGRESSION BETWEEN SEED MASS, AND MEDIAN GERMINATION TIME

According to the regression plot, the R^2 value in 2017 was approximately 4% (Fig. 4a), indicating that seed mass accounted for 4% of the variability in t_{50}, with a slope of –0.35. This explains that any increase in seed mass possibly reduces t_{50} by up to

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4.68 days. According to 2022 plot, the R^2 value was about 12% for seed mass, meaning that seed mass accounted for 12% of the variability in t_{50}, with the slope up to −1.35. Consequently, any increase in seed mass could directly shorten t_{50} by up to 6.56 days, requiring more time to reach t_{50} compared to seeds collected during the wet period of 2017 (Fig. 4b).

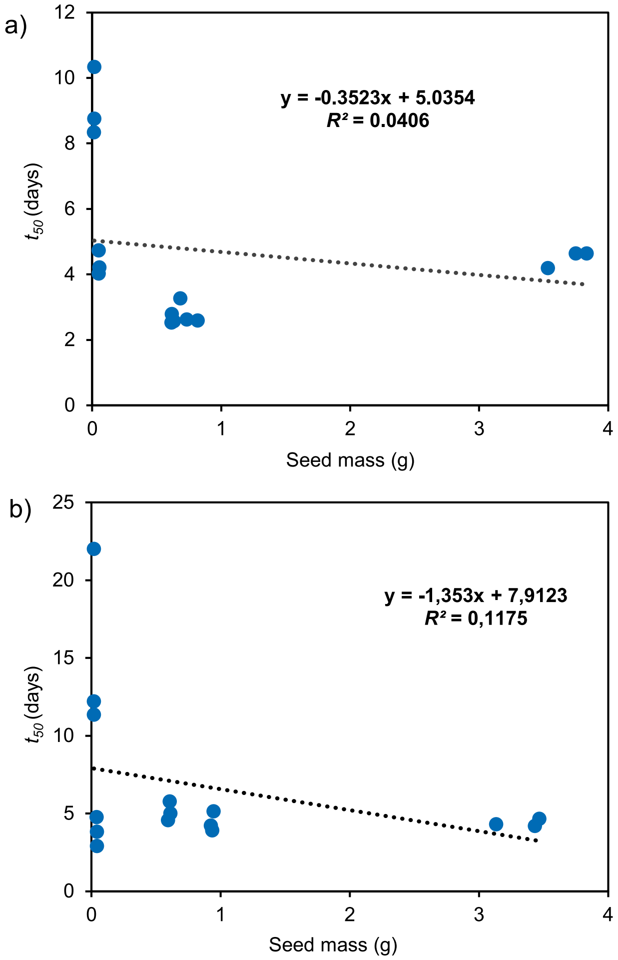

Fig. 4. Regression plots between seed mass (g) – median germination time (t_{50}): a) 2017, b) 2022; explanations: R^2 = coefficient of determination; source: own study

In previous studies, seed mass acted was a major variable for predicting most aspects of germination, including germination time (Masuda and Washitani, 1990). In this study, linear regression plots were established with seed mass as the independent variable and germination time (t_{50}) as the dependent variable for two sourcing years (2017 and 2022). The duration of emergence time has been linked to increased germination velocity, which results from optimal energy utilisation of nutrient storage in seeds. Consequently, rapid energy synthesis in large-seeded species creates trade-offs compared to small-seeded species, specifically among perennial plants. This advantage allows large-seeded species to establish dominance earlier, narrowing the germination window for small-seeded species (Verdú and Traveset, 2005).

These findings validate the developed establishment equations from this study, which can be applied to optimise sowing strategies, including seed quantity and sowing timing to enhance seedling establishment. Furthermore, further studies should be conducted to re-evaluate the equations under changing climatic conditions in field settings.

CONCLUSIONS

Two different climatic regimes during seed collection led to significant variations in germination performance across the five selected plant species. Although seed mass did not exhibit a statistically significant response, a decrease of this parameter was found in most species. This finding demonstrated that seed mass responds differently depending on species-specific factors under different climatic conditions. This study confirmed the assumption that species with larger seeds exhibit higher germination capacity and germination velocity.

Finally, according to the developed equations, seed mass in the selected species contributed to a shorter germination time, facilitating rapid emergence and influencing plant establishment. Based on the results obtained, we can recommend some species for seed-based restoration. *Tragopogon pratensis* is most suitable for restoration, while *Campanula patula* is the least useful, regardless of the year. The suitability of other species varies depending on climatic conditions: *Centaurea jacea* and *Plantago lanceolata* are more suitable in dry seasons, whereas *Achillea millefolium* in wet seasons.

CONFLICT OF INTERESTS

All authors declare that they have no conflict of interests.

REFERENCES

Cappers, R.T.J., Bekker, R.M. and Jans, J.E.A. (2006) *Digitale Zadenatlas van Nederland [Digital seed atlas of the Netherlands]*. Groninger: Barkhuis Publishing and Groningen University Library.

Council Directive (1992) “Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora,” *Official Journal*, L 206. Consolidated version 1.7.2013.

Dalgleish, H.J., Koons, D.N. and Adler, P.B. (2010) “Can life-history traits predict the response of forb populations to changes in climate variability?,” *Journal of Ecology*, 98, pp. 209–217. Available at: https://doi.org/10.1111/j.1365-2745.2009.01585.x.

Donohue, K. *et al.* (2010) “Germination, postgermination, adaptation, and species ecological ranges,” *Annual Review of Ecology, Evolution, and Systematics*, 41, pp. 293–319. Available at: https://doi.org/10.1146/annurev-ecolsys-102209-144715.

Dudney, J. *et al.* (2017) “Lagging behind: Have we overlooked previous-year rainfall effects in annual grasslands?” *Journal of Ecology*, 105, pp. 484–495. Available at: https://doi.org/10.1111/1365-2745. 12671.

Dukes, J. *et al.* (2011) “Strong response of an invasive plant species (*Centaurea solstitialis* L.) to global environmental changes,” *Ecological Applications*, 21(6), pp. 1887–1894. Available at: https://doi.org/10.1890/11-0111.1.

EEA (2019) *Lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis). EUNIS – Factsheet for lowland hay meadows (Alopecurus pratensis, Sanguisorba officinalis)*. Copenhagen:

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European Environment Agency. Available online: https://eunis.eea.europa.eu/habitats/10137 (Accessed: August 26, 2024).

Ellenberg, H. and Leuschner, Ch. (2010) *Vegetation Mitteleuropas mit den Alpen [Vegetation of Central Europe with the Alps]*. 6th edn. Stuttgart: Eugen Ulmer Verlag, UTB.

Farooq, M. *et al.* (2005) "Thermal hardening: A new seed vigor enhancement tool in rice," *Journal of Integrative Plant Biology*, 47, pp. 187–193. Available at: https://doi.org/10.1111/j.1744-7909.2005.00031.x.

Fay, P.A. and Schultz, M.J. (2009) "Germination, survival, and growth of grass and forb seedlings: Effects of soil moisture variability," *Acta Oecologica*, 35, pp. 679–684. Available at: https://doi.org/10.1016/j.actao.2009.06.007.

Fenner, M. and Thompson, K. (2005) *The ecology of seeds*. New York: Cambridge University Press.

Fernández-Pascual, E. *et al.* (2022) "Seed ecology of European mesic meadows," *Annals of Botany*, 129, pp. 121–133. Available at: https://doi.org/10.1093/aob/mcab135.

Fry, E.L., Manning, P. and Power, S.A. (2014) "Ecosystem functions are resistant to extreme changes to rainfall regimes in a mesotropic grassland," *Plant Soil*, 381, pp. 351–365. Available at: https://doi.org/10.1007/s11104-014-2137-2.

Hölzel, N. and Otte, A. (2004) "Assessing soil seed bank persistence in flood-meadows: The search of reliable traits," *Journal of Vegetation Science*, 15, pp. 93–100. Available at: https://doi.org/10.1111/j.1654-1103.2004.tb02241.x.

ISTA (2018) *Międzynarodowe przepisy oceny nasion ISTA, 2018 wersja polska [International rules for seed testing, Polish version].* Radzików, Poland: IHAR-PIB.

Jäger, H. *et al.* (2020) "Grassland biomass balance in the European Alps: Current and future ecosystem service perspectives," *Ecosystem Services*, 45, 101163. Available at: https://doi.org/10.1016/j.ecoser.2020.101163.

Janicka, M. *et al.* (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. Available at: https://doi.org/10.3390/su132413979.

Janicka, M., Pawluśkiewicz, B. and Gnatowski, T. (2023) "Preliminary results of the introduction of dicotyledonous meadow species," *Sustainability*, 15, 3231. Available at: https://doi.org/10.3390/su15043231.

Kiss, R. *et al.* (2018) "Grassland seed bank and community resilience in a changing climate," *Restoration Ecology*, 26, pp. S141–S150. Available at: https://doi.org/10.1111/rec.12694.

Koutsovoulou, K., Daws, M.I. and Thanos, C.A. (2014) "Campanulaceae: A family with small seeds that require light for germination," *Annals of Botany*, 113, pp. 135–143. Available at: https://doi.org/10.1093/aob/mct250.

Kövendi-Jakó, A. *et al.* (2017) "Relationship of germination and establishment for twelve plant species in restored dry grassland," *Applied Ecology and Environmental Research*, 15(4), pp. 227–239. Available at: http://dx.doi.org/10.15666/aeer/1504_227239.

Masuda, M. and Washitani, I. (1990) "A comparative ecology of the seasonal schedules for 'Reproduction by seeds' in a moist tall grassland community," *Functional Ecology*, 4(2), pp. 169–182. Available at: https://doi.org/10.2307/2389336.

Mirek, Z. *et al.* (2020) "Krytyczna lista roślin naczyniowych Polski [Flowering plants and pteridophytes of Poland – A checklist]," in Z. Mirek and W. Szafer (eds.) *Bioróżnorodność Polski [Biodiversity of Poland]*. Kraków: Institute of Botany, Polish Adacemy of Sciences, Vol. 1.

Murray, B.R. *et al.* (2004) "Geographical gradients in seed mass in relation to climate," *Journal of Biogeography*, 33, pp. 379–388. Available at: https://doi.org/10.1046/j.0305-0270.2003.00993.x.

O'Brien, M. *et al.* (2013) "The influence of variable rainfall frequency on germination and early growth of shade-tolerant Dipterocarp seedlings in Borneo," *PLoS ONE*, 8(7), e70287. Available at: https://doi.org/10.1371/journal.pone.0070287.

Rosbakh, S. *et al.* (2022) "Alpine plant communities differ in their seed germination requirements along a snowmelt gradient in the Caucasus," *Alpine Botany*, 132, pp. 223-232. Available at: https://doi.org/10.1007/s00035-022-00286-x.

Schils, R.L.M. *et al.* (2022) "Permanent grasslands in Europe: Land use change and intensification decrease their multifunctionality," *Agriculture, Ecosystem and Environment*, 330, 107891. Available at: https://doi.org/10.1016/j.agee.2022.107891.

Seguí, N., Jiménez, M.A. and Cursach, J. (2021) "Local conditions effects on seed germination of *Hypericum balearicum* L. in response to temperature," *Flora*, 282, 151896. Available at: https://doi.org/10.1016/j.flora.2021.151896.

Timson, J. (1965) "New method of recording germination data," *Nature*, 207, pp. 216–217. Available at: https://doi.org/10.1038/207216a0.

Verdú, M. and Traveset, A. (2005) "Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis," *Ecology*, 86 (6), pp. 1385–1394. Available at: https://doi.org/10.1890/04-1647.

Veselá, A. *et al.* (2020) "Seed mass and plant home site environment interact to determine alpine species germination patterns along an elevation gradient," *Alpine Botany*, 130, pp. 101–113. Available at: https://doi.org/10.1007/s00035-020-00242-7.

Vinczeffy, I. (1984) "The effect of some ecological factors on grass yield," in *Proceedings of the 10th General Meeting of European Grassland Federation*, 26–30 June 1984. Ås, Norway: Norwegian State Agricultural Research Stations, pp. 76–79.

Wang, Y. *et al.* (2018) "Phylogeny, habitat together with biological and ecological factors can influence germination of 36 subalpine *Rhododendron* species from the eastern Tibetan Plateau," *Ecology and Evolution*, 8, pp. 3589–3598. Available at: https://doi.org/10.1002/ece3.3874.

Xu, J. and Du, G. (2023) "Seed germination response to diurnally alternating temperatures: Comparative studies on alpine and subalpine meadows," *Global Ecology and Conservation*, 44, e02503. Available at: https://doi.org/10.1016/j.gecco.2023.e02503.

Yi, F. *et al.* (2019) "Seed germination responses to seasonal temperature and drought stress are species-specific but not related to seed size in a desert steppe: Implications for effect of climate change on community service," *Ecology and Evolution*, 9, pp. 2149–2159. Available at: https://doi.org/10.1002/ece3.4909.

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