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Modelling the Effects of Warmer, Drier Winters on Dormancy Release and Germination in Summer Annual Weeds

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ABSTRACT

We investigated how increasing temperatures and drought may impact plant communities through interactions with seed dormancy and germination patterns. Soil temperatures (2°C, 5°C and 8°C) and water potentials (−0.3, −0.9 and −1.5 MPa) were simulated during a 6-month burial period for the five summer annual species *Amaranthus blitoides* S. Watson, *Diplachne fusca* L. P. Beauv. ex Roem. & Schult, *Echinochloa crus-galli* L. P. Beauv, *Polygonum aviculare* L. and *Solanum nigrum* L. Seeds were retrieved every 30 days and germinated at temperatures ranging from 10°C to 40°C. Burial duration was the primary driver of variation in cumulative germination fractions, followed by incubation temperature. While soil temperature contributed less than other factors to germination variation, increasing soil temperature consistently had a positive effect on germination across all species. *Amaranthus blitoides* was only marginally affected by soil moisture, whereas *P. aviculare*, *S. nigrum*, *E. crus-galli* and *D. fusca* were significantly influenced by it, with *P. aviculare* being the most sensitive and *D. fusca* the least. Notably, *D. fusca* and *E. crus-galli* exhibited low rates of germination even after shorter burial durations when incubation temperatures were within a favourable range. This suggests that suitable post-burial thermal conditions can support some germination, even when dormancy break is incomplete. Regarding thermal parameters, the ceiling temperature (T_c) increased slightly during dormancy break, while the base temperature (T_b) showed more pronounced changes. The prediction model suggests that species less dependent on soil moisture and temperature, such as *A. blitoides*, may maintain or expand their ranges under warmer, drier winters, whereas moisture-sensitive species like *P. aviculare* may experience range contraction. Climate-driven changes in soil temperature and moisture are thus likely to alter germination success and by this reshape future plant communities.

1 | Introduction

The establishment of annual plant species primarily depends on successful seed germination, influenced by internal and environmental factors. To ensure germination occurs at the right time, seeds must possess traits that allow them to sense and respond to environmental conditions effectively (Soltani et al. 2022). Non-deep physiological dormancy is an adaptive trait that has evolved to ensure a species' survival in specific environments (Baskin and Baskin 2023). This type of dormancy responds to local environmental cues signalling the optimal time for germination, and is influenced by soil temperature and moisture, which can either promote or inhibit germination (Egley 2017). Once seeds are shed, they encounter fluctuating temperatures and moisture levels. For example, seeds of summer annuals dispersed in early autumn experience low temperatures through autumn and winter, followed by increasing temperatures in spring, the optimal time for germination. Over generations, natural selection favours individuals tolerant of these conditions, shifting population dynamics toward those more tolerant of environmental changes (Doohan et al. 2003). Dormancy release typically aligns with historical climate patterns, occurring during the season unfavourable for seedling growth, resulting in seeds being non-dormant at the start of the favourable growth season (Bernareggi et al. 2016).

Non-deep physiological dormancy acts as a 'closed window', preventing germination under conditions unfavourable for seedling establishment. This window gradually opens over time in response to environmental cues such as soil temperature and moisture, while additional factors, such as light exposure or physical scarification, may further accelerate the process. Hereafter, we use the term dormancy break to denote the progressive loss of physiological dormancy, that is, the gradual increase in a seed's propensity to germinate in response to appropriate environmental cues. In many species, dormancy break is primarily induced by cold stratification, during which moist seeds exposed to low but nonfreezing temperatures undergo physiological adjustments, including decreased abscisic acid (ABA) concentrations, enhanced gibberellin (GA) activity and increased embryo growth potential (Yang et al. 2019). These processes enhance seed responsiveness to favourable germination conditions, allowing the accumulation of sufficient thermal time (TT) for successful germination and seedling establishment (Baskin and Baskin 2020).

The hydrothermal time (HTT) model effectively captures how germination responsiveness is governed by two key environmental parameters—temperature and moisture—by quantifying how deviations from their respective threshold values affect germination rate (Bradford and Bello 2022). In this framework, the germination rate for a seed population is determined by the extent to which prevailing temperature and water potential (a measure of soil moisture stress) exceed these thresholds. Soil temperature and moisture thus play critical roles not only in dormancy break but also in subsequent germination dynamics. Consequently, within a given location, shifts in these environmental factors due to climate change can alter species abundance patterns: in arid regions, species adapted to higher temperatures and drought may become more dominant, while those dependent on cooler or moister conditions may decline (Hufnagel and Garamvölgyi 2014).

Climate change, particularly warmer and drier winters, disrupts the dormancy-germination cycle of many species. Two main hypotheses explain these effects. Warmer temperatures may prevent species from meeting their cold stratification requirements leading to prolonged dormancy and delayed germination (Reed et al. 2022). Alternatively, higher temperatures may provide the necessary base temperature earlier, accelerating germination (Notarnicola et al. 2023). However, dormancy release is highly species-specific, and responses to temperature and moisture will vary among species (Hu et al. 2018).

The temperature range for dormancy break by cold stratification (typically 0°C–10°C, with 5°C being optimal) varies among species. For example, C_3 species require about 1551 ± 48.6 h of cold stratification, while C_4 species require about 1727.7 ± 69.5 h. Then, the time required for germination to begin is approximately 80.8 ± 1.7 h for C_3 species and 87.4 ± 1.7 h for C_4 species (Baskin and Baskin 2022). Temperature effects on dormancy break are time-dependent, requiring enough cold days to accumulate necessary stratification. Moisture also plays a critical role in this process.

Species with strong cold stratification requirements, like *C. album* L. and *P. aviculare* L., may experience prolonged dormancy and delayed spring germination due to insufficient cold exposure (Tang et al. 2008; Batlla et al. 2009). Although natural selection can, over longer timescales, favour individuals with reduced chilling requirements, the rapid pace of current climate change may outstrip this adaptive potential. In the short term, insufficient cold stratification could cause staggered or irregular germination, reducing establishment success. Similarly, drought-sensitive species, such as *A. retroflexus* L. and *E. crus-galli* (L.) P. Beauv, may face delayed germination in drier winters due to both shortened stratification periods and inadequate hydration to respond to stratification cues (Safavi et al. 2023; Wu et al. 2019).

Conversely, species with low cold stratification requirements, such as *A. blitoides* and *S. nigrum*, may lose dormancy more quickly under warmer winters and germinate earlier than species with stronger stratification needs. However, this could expose seedlings to early-season stressors. These species may also depend on other environmental factors, such as soil moisture, to break dormancy and initiate germination (Talaee et al. 2024; Dong et al. 2020). Moisture-dependent species, like *D. fusca*, may experience significant germination delays if moisture is insufficient, even if cold stratification requirements are met (Snow et al. 2018).

To investigate these interactions, five summer annual species with known varying levels of non-deep physiological dormancy were selected: *A. blitoides*, *D. fusca* and *E. crus-galli* (low dormancy) and *P. aviculare* and *S. nigrum* (moderate dormancy). Low dormancy refers to seeds that germinate readily under favourable conditions, with minimal or no requirement for after-ripening, stratification, or other dormancy-breaking cues. Moderate dormancy refers to seeds that require specific

environmental signals such as temperature fluctuations, light exposure, or after-ripening to germinate (Nautiyal et al. 2023). After-ripening is an environmentally modulated physiological process that takes place in desiccated seeds, ultimately defining their capacity for germination (Carrera et al. 2008). All species are common weeds in summer crops and widely distributed in agricultural regions. The objective was to evaluate their germination responses under different temperature and soil moisture conditions during the seed burial period. For this purpose, a predictive model was developed using soil moisture and temperature data collected during burial, estimating accumulated thermal time and cumulative germination fractions and identifying key parameters influenced by the experimental conditions.

2 | Materials and Methods

Seeds of *A. blitoides*, *E. crus-galli*, *S. nigrum* and *P. aviculare* were collected from the University of Tehran research farm in Karaj, Iran (35°48′ N and 50°57′ E). Seeds of *D. fusca* were collected from sugarcane farms in Khuzestan (31°18′ N and 48°40′ E). To ensure a random parental plant effect, seeds were collected from at least 50 mature plants of each species from various locations, including fields, margins and roadsides, and stored in a paper bag at room temperature (20°C–25°C) for about a month until the experiment began. The moisture content of seeds for all species was between 9% and 11%.

The experiment followed a factorial design with the five plant species *Amaranthus blitoides*, *Echinochloa crus-galli*, *Solanum nigrum*, *Polygonum aviculare* and *Diplachne fusca*, three soil moisture levels (−0.3, −0.9 and −1.5 MPa), three soil temperatures (2°C, 5°C and 8°C), six burial durations (1–6 months) and seven germination test temperatures (10°C–40°C, at 5°C intervals), resulting in 1890 treatment combinations. Each treatment included four replicates, giving a total of 7560 chiffon bags, each containing 50 seeds. The chiffon bags (60 mesh per inch) ensured adequate soil contact during burial (Figure 1).

Soil moisture levels of −0.3, −0.9 and −1.5 MPa were established using a pressure plate apparatus. Soil samples were air-dried, sieved through a 2 mm mesh to obtain a uniform texture and approximately 500 g of soil was placed into porous stainless-steel rings compatible with the pressure plate setup. The soil was saturated with deionised water to eliminate air pockets, then placed on pre-saturated ceramic plates inside the pressure chamber. The chamber was sealed and pressurised to the target matric potentials, with equilibration times ranging from 24 to 36 h depending on pressure level. After equilibration, pressure was gradually released, and the samples were weighed to determine gravimetric water content. Pots were subsequently filled with soil at the designated moisture levels and weighed to ensure consistency.

Soil was collected from the 0–20 cm layer at the research farm of the University of Tehran, Karaj, Iran. It was classified as clay loam (40% sand, 35% silt, and 25% clay), with pH 7.2 (1:2.5 soil:water), 1% organic matter, bulk density 1.3 g cm^{-3}, cation exchange capacity (CEC) 12 cmolc kg^{-1} and electrical conductivity (EC) of the saturated extract 0.25 dS m^{-1}. Total nitrogen content (Kjeldahl method) was 0.08%, while available

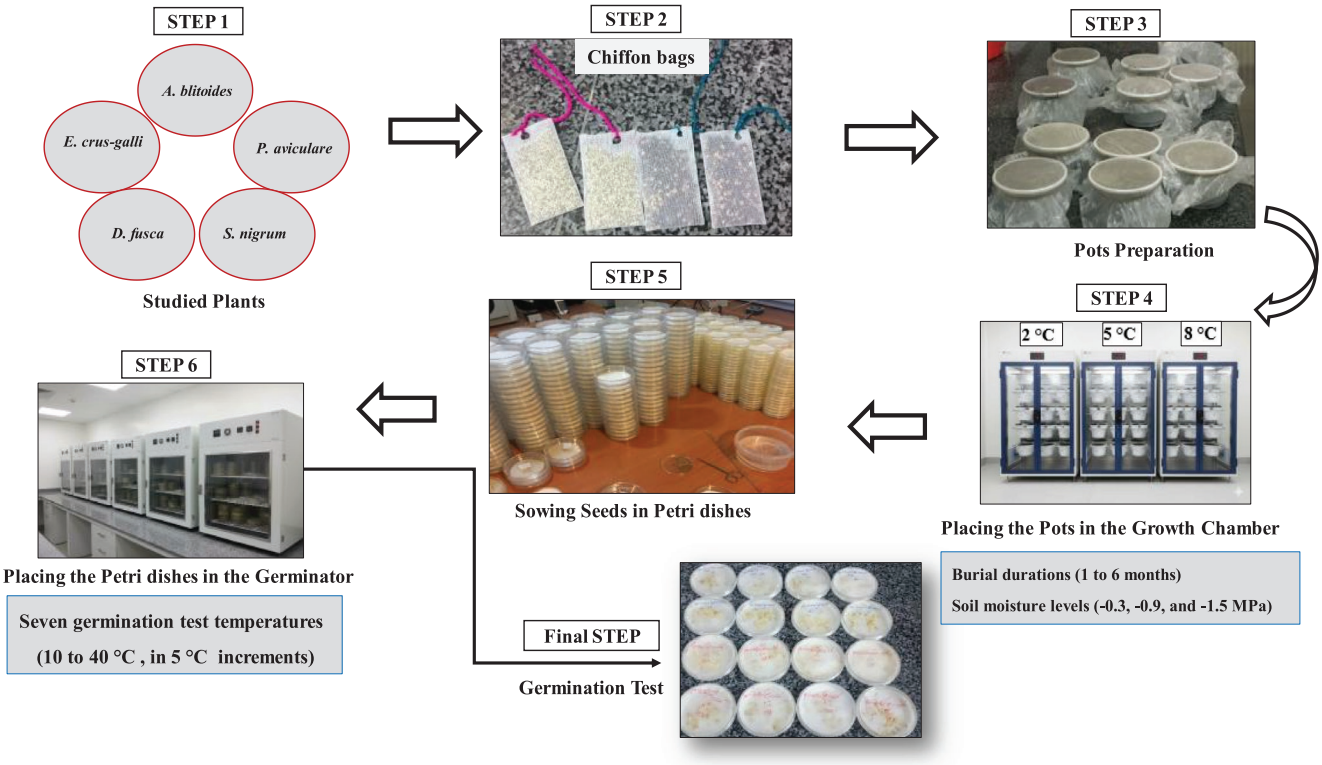


FIGURE 1 | Overview of the experimental procedure used to evaluate treatment effects on dormancy release and germination responses of the study species.

phosphorus (Olsen-P) and exchangeable potassium (K) were 15 and 180 mg kg^{-1}, respectively. Before use, soil was air-dried, sieved (2 mm) and homogenised to ensure uniform properties across treatments.

Because water uptake (imbibition) and the hydric cue for dormancy break depend on the difference between seed water potential and the surrounding medium, we selected −0.3, −0.9 and −1.5 MPa to span an ecologically meaningful gradient (mild → moderate → severe water limitation) that has been widely used to test drought effects on imbibition and germination (Dürr et al. 2015; Chen et al. 2022).

Imbibition dynamics and the threshold water content required for radicle protrusion are species-specific, owing to differences in seed coat permeability, seed mass and intrinsic embryo water potential; therefore the moisture gradient was chosen specifically to reveal species × moisture interactions, that is, different species may lose the ability to imbibe or to translate imbibition into germination at different matric potentials. Empirical studies show consistent interspecific variation in imbibition kinetics and base water potentials for germination, supporting our expectation of species-specific responses (Pompelli et al. 2023; Gómez-Maqueo et al. 2020). To verify the stability and comparability of the moisture treatments we (i) confirmed gravimetric water content after equilibration for each pressure level, (ii) used identical soil texture and ring volume to reduce matrix variability and (iii) included species × moisture interaction terms in our statistical models so that interspecific variation in imbibition/germination could be explicitly tested. These procedural checks reduce the likelihood that observed differences are artefacts of the moisture manipulation (Moret-Fernández et al. 2023).

During the burial of the seeds, pot weights were monitored. If a sealed pot lost water below the experimental soil moistures, water was added to maintain consistent soil moisture. The pots were labelled and stored in growth cabinets set at 2°C, 5°C and 8°C for 6 months. At 30-day intervals, seeds from each species and treatment were tested for germination at constant temperatures ranging from 10°C to 40°C (in 5°C increments). For *D. fusca*, an additional test at 45°C was included, given previous evidence of its ability to germinate at this temperature (Ebrahimi 2014). Germination tests were conducted in incubators set at the experimental temperatures, with a 12-h light (15 μmol m^{-2} s^{-1})/12-h dark cycle (Jha et al. 2010). Seed germination was counted over 336 h (14 days) at 24-h intervals. Although fluctuating temperatures better reflect ecological realism, constant incubation temperatures were used to prevent confounding effects on thermal time calculations and ensure consistent comparisons across treatments and species. The cumulative germination fraction (*CGF*) for each species was calculated for further analysis.

2.1 | Model Development

We developed a mechanistic model that incorporates the combined effects of soil burial duration, soil temperature, soil moisture and incubation temperature to predict cumulative germination fractions (*CGF*) over time (Figure 2). The Triangle Area Model (*TAM*) approach (Oveisi et al. 2024) estimates the thermal time (*TT*) required for seed germination under a range of environmental conditions. This approach conceptualises *TT* accumulation as the area of a right-angled triangle, where the base represents time progression driven by temperature and the height corresponds to the germination response at a given time and temperature.

The calculation of the triangle's base differs between sub-optimal and supra-optimal temperature conditions. Specifically, for sub-optimal conditions, where the temperature is below the optimum ($T < T_o$), the base is computed as:

$$Base_{sub} = (T - T_b) \times t_g \quad (1)$$

and for supra-optimal conditions where temperature is above the optimum:

$$Base_{sup} = (T_c - T) \times t_g \quad (2)$$

The height of the triangle, denoted as $G(t)$, represents the cumulative germination fraction at time t and temperature T. The maximum germination fraction under optimal conditions is denoted G_m. To account for declining germination efficiency as temperatures deviate from the optimum, two coefficients are introduced to scale the height of the triangle, one for sub-optimal and one for supra-optimal temperatures (Oveisi et al. 2024):

$$HA_{subT} = HA_{sub} \times \left(1 - \frac{(T_o - T)}{(T_o - T_b)}\right) \quad (3)$$

$$HA_{supT} = HA_{sup} \times \left(1 - \frac{(T - T_o)}{(T_c - T_o)}\right) \quad (4)$$

where HA_{sub} and HA_{sup} are baseline coefficients representing the decline in efficiency on either side of the optimal temperature (T_o). So with the T distant from the optimal temperatures, HA_{sub} and HA_{sup} decrease.

Seed dormancy break and germination potential are also influenced by soil temperature (*ST*), soil moisture (*SM*) and burial time (*BT*) during seed bank persistence. These environmental drivers modulate $G(t)$ through the following empirical relationships:

$$G_{ST} = b_0 - b_1 \times ST \quad (5)$$

$$G_{SM} = c_0 + c_1 \times SM \quad (6)$$

$$G_{BT} = \frac{G_{max}}{1 + \left(\frac{BT}{BT_{50}}\right)^{b_{BT}}} \quad (7)$$

where G_{ST} is $G(t)$, which linearly changes with *ST*, G_{SM} is the $G(t)$ value which linearly affected by *SM*, G_{BT} is the $G(t)$ which sigmoidally change with burial time. b_0 represents the intercept, and b_1 represents the rate of increase in G_{ST} as *ST* increases. C_0 is the intercept, and C_1 is the rate of increase in $G(t)$ with increasing *SM*. G_{max} is the asymptotic germination fraction, BT_{50} is the

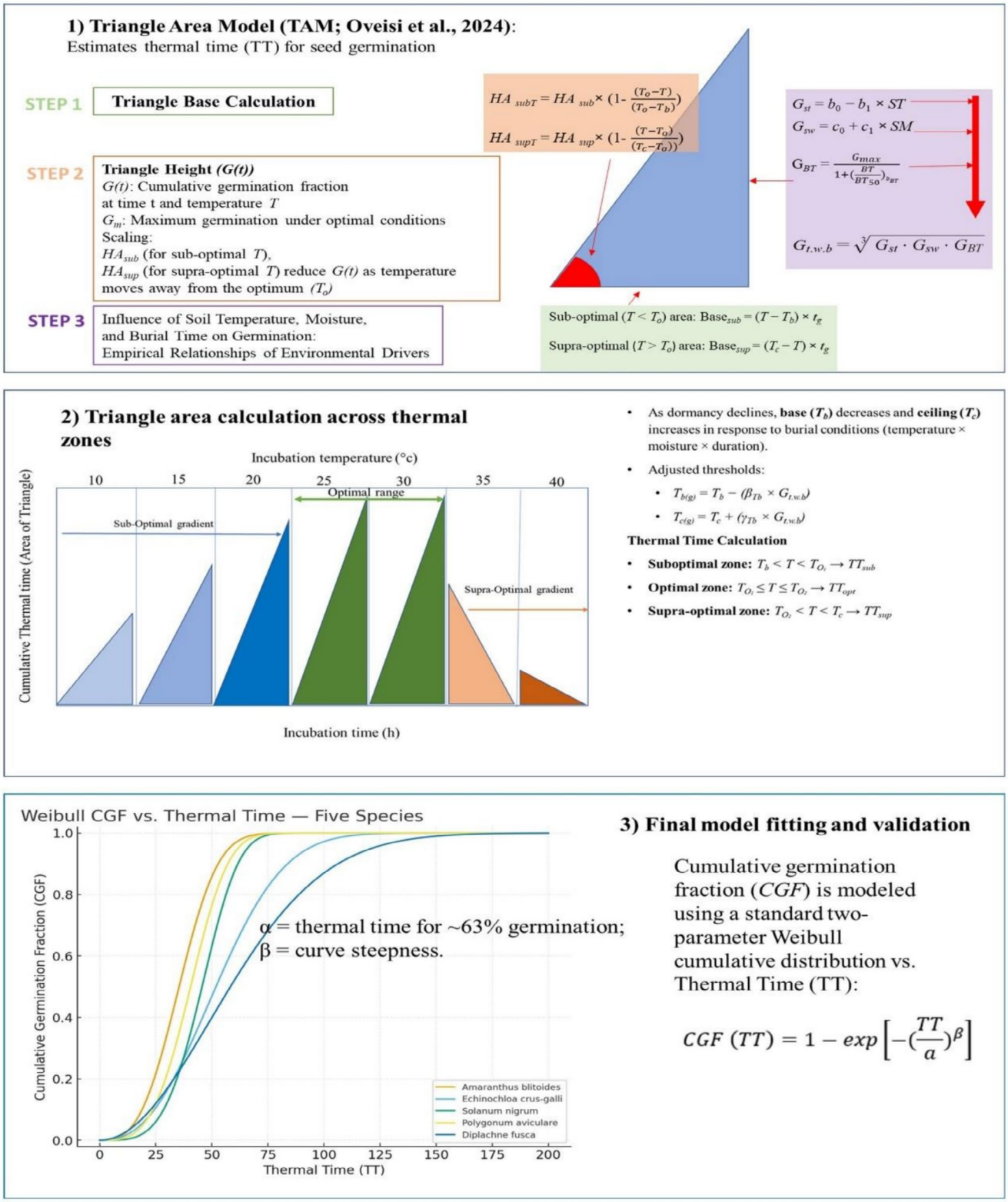


FIGURE 2 | Schematic illustration of the concept, development and formulations of the model.

burial time at which 50% of G_{max} is reached and b_{BT} is the slope (Olvera-Carrillo et al. 2009).

After exploring various approaches to combine the effects of soil moisture, soil temperature and burial time on germination such as linear weighting, multiplicative models and several types of averaging the geometric mean provided the best overall fit to observed data and biological expectations. This conclusion was reached following an extensive trial-and-error process comparing model performances, where the geometric mean most effectively captured

the interactive and non-linear nature of environmental effects on seed dormancy break and germination potential. Hence, the combined effect of these factors is expressed as:

$$G_{t\cdot w\cdot b} = \sqrt[3]{G_{ST} \cdot G_{SM} \cdot G_{BT}} \tag{8}$$

as seeds lose dormancy with environmental exposure over time, their thermal thresholds dynamically shift (Liyanage and Ooi 2017). To account for this, T_b and T_c are allowed to vary according to the accumulated effect of burial conditions:

$$T_{b(g)} = T_b - \left(\beta_{Tb} \cdot G_{t\cdot w\cdot b}\right) \tag{9}$$

$$T_{c(g)} = T_c + \left(\gamma_{Tb} \cdot G_{t\cdot w\cdot b}\right) \tag{10}$$

where β_{Tb} and γ_{Tb} are coefficients representing the influence of soil temperature and moisture conditions over time on T_b and T_c, respectively. We also assume the existence of an optimal temperature range within which seeds germinate most efficiently. This range is bounded by T_{O1} and T_{O2}, representing the lower and upper limits of the optimum, respectively, and is assumed to remain constant over time (Soltani et al. 2016). Accordingly, germination time is divided into three cardinal temperature zones, and TT is calculated separately for each zone.

Suboptimal zone ($T_b < T < T_{O1}$):

$$TT_{sub} = \frac{\left(T - T_{b(g)}\right) \cdot HA_{sub} \cdot G_{t\cdot w\cdot b} \cdot t}{2}$$

Optimal zone ($T_{O1} \le T \le T_{O2}$):

$$TT_{opt} = \frac{\left(T - T_{o1}\right) \cdot G_{t\cdot w\cdot b} \cdot t}{2} \tag{11}$$

Supra-optimal zone ($T_{O2} < T < T_c$):

$$TT_{sup} = \frac{\left(T_{b(g)} - T_{O2}\right) \cdot HA_{sup} \cdot G_{t\cdot w\cdot b} \cdot t}{2}$$

the cumulative germination fraction (CGF) was modelled using a standard two-parameter Weibull cumulative distribution function based on thermal time (TT) for each thermal region.

$$CGF\,(TT) = 1 - \exp\left[-\left(\frac{TT}{a}\right)^{\beta}\right] \tag{12}$$

where α (alpha) is the scale parameter (the thermal time at which approximately 63.2% of seeds have germinated), and β (beta) is the shape parameter, which defines the steepness of the germination curve.

2.2 | Statistical Methods

The Response Screening (RS) platform in JMP (SAS Institute 2016) was used to identify which experimental factors best explained variation in the germination fraction (g) across our dataset, including plant species, burial duration, burial-soil moisture, burial-soil temperature, incubation temperature and germination time. The RS platform performs multiple univariate tests across responses and reports the LogWorth statistic (defined as $-\log_{10}(p\text{-value})$) to rank the relative significance of predictors, where a LogWorth >2 corresponds to $p<0.01$ (Morris 1991). This exploratory screening procedure implements False Discovery Rate (FDR) control to reduce false positives arising from multiple testing and is therefore suitable for experiments involving numerous germination factors (Oveisi et al. 2025).

The germination rate (GR, h^{-1}) was calculated as the inverse of the time required to reach 30% germination. This threshold was chosen because it was achieved in at least one replicate for every treatment combination (5 species × 6 burial times × 3 temperatures × 3 moisture levels; total = 486), allowing standardised rate comparisons (Bradford and Bello 2022). A four-parameter Weibull function was fitted to the CGF versus germination time (h) to estimate GR, and the parameter estimates predicting the germination fractions of the study species were calculated (Table 1). To estimate the temperature thresholds controlling seed germination across environmental treatments, a two-segment linear thermal time model (Hardegree 2006) was fitted to germination rate data (GR_{30}, i.e., the inverse of time to 30% germination) as a function of incubation temperature (T). The model estimates two cardinal temperature parameters: base temperature (T_b) and ceiling temperature (T_c), following a piecewise linear formulation.

$$GR(T): \begin{cases} 0 & \text{If } T \le T_b \text{ or } T \ge T_c \\ \dfrac{(T - T_b)}{(T_o - T_b)} & \text{if } T_b < T \le T_o \\ \dfrac{(T_c - T)}{(T_c - T_o)} & \text{if } T_o < T < T_c \end{cases} \tag{13}$$

This two-segment model assumes that the germination rate increases linearly with temperature up to an optimum (T_o), then declines linearly to zero at the ceiling temperature (T_c). This reflects the unimodal response of the germination rate to temperature without a plateau phase.

To fit the model, nonlinear least squares optimisation was performed via the *optim*() function in *R*, with the L-BFGS-B algorithm applied for parameter bounding. The following bounds were applied: T_b: 0°C–15°C, T_o: 10°C–35°C and T_c: 25°C–50°C.

The root mean square error ($RMSE$) between observed and predicted germination rates was minimised. The coefficient of determination (R^2) was calculated to assess model fit. To evaluate predictive accuracy and the robustness of parameter estimates, 10-fold cross-validation was performed using the *createFolds*() function from the caret package, with each model trained on 90% of the data and validated on the remaining 10%. Performance was assessed using:

$$RMSE = \sqrt{\frac{1}{n}\sum\left(y_i - \hat{y}_i\right)^2} \tag{14}$$

TABLE 1 | Parameter estimates for the model predicting germination fractions across study species.

Parameter estimates	*A. blitoides*	*E. crus-galli*	*P. aviculare*	*D. fusca*	*S. nigrum*
T_b	14.16	5.70	4.10	19.68	6.19
T_{O1}	20.00	19.88	14.09	23.11	25.99
T_{O2}	25.90	33.19	27.29	28.53	29.64
T_c	45.40	43.10	49.58	46.33	49.32
HA_{sub}	4.97	0.48	10.22	0.00	18.32
HA_{sup}	6.61	14.06	14.80	9.23	15.34
G_{max}	715.03	573.51	1509.02	1208.80	680.41
BT_{50}	163.11	198.14	151.72	140.19	184.91
b_{BT}	−6.07	−4.60	−4.31	−6.07	−4.46
c_0	53.68	213.01	89.99	166.98	80.44
c_1	18.50	105.91	54.74	103.64	46.78
b_0	285.99	1153.79	548.91	771.25	522.59
b_1	−1.21	−2.48	−20.70	13.90	−19.24
Alpha	1.52	1.69	1.44	1.42	1.43
Beta	95 534.12	74 481.76	96 110.76	62 561.17	88 412.61
Adj_R²	0.911	0.817	0.889	0.876	0.882
RMSE	0.043	0.075	0.057	0.051	0.055
MBE	−0.001	−0.003	−0.003	−0.003	−0.002

Note: T_b: base temperature; T_{O1}: lower optimal temperature; T_{O2}: upper optimal temperature; T_c: ceiling temperature; HA_{sub} and HA_{sup}: baseline coefficients representing the decline in efficiency on either side of the optimal temperature; G_{max}: asymptotic germination fraction; BT_{50}: burial time at which 50% of G_{max} is reached; b_{BT}: slope. c_0: intercept; c_1: rate of increase in $G(t)$ with increasing soil moisture; b_0: intercept; b_1: rate of increase in $G(t)$ with increasing soil temperature. α (*alpha*): scale parameter, representing the thermal time at which approximately 63.2% of seeds have germinated; β (*beta*): shape parameter, defining the steepness of the germination curve. Adj_R^2: Adjusted coefficient of determination; *RMSE*: root mean square error; *MBE*: mean bias error.

$$MBE = \frac{1}{n}\sum_{i=1}^{n}\left(P_i - O_i\right) \tag{15}$$

$$Adj - R^2 = 1 - \left(\frac{n-1}{n-p-1}\right)\left(1 - R^2\right) \tag{16}$$

where n is the number of observations, y_i is the actual value, $\hat{y}_i$ is the predicted value by the model for the ith observation, and O_i is the observed (or actual) value for the ith observation. A positive *MBE* indicates that the model overestimates observed values, while a negative *MBE* indicates underestimation. The closer the *MBE* is to zero, the better the model's predictions align with actual observations. The dataset was randomly partitioned into training, validation and test subsets to assess the model's robustness. Data analysis, model development and graphing were performed in R-studio (v2023.03.1) and JMP Pro 17.

3 | Results

3.1 | Germination Response to Treatments

Across all species, soil temperature generally had low to marginal effects, with its relative contribution ranking as follows: *S. nigrum* > *P. aviculare* > *E. crus-galli* > *D. fusca*. Response surface analysis revealed that burial time was the primary driver of variation in germination fractions, significantly influencing other experimental factors. Incubation temperature, soil moisture, plant species and soil temperature followed in descending order of importance (Figure 3a). Within species, the relative contribution of each factor to seed germination varied. In *A. blitoides*, burial duration was the most influential factor, followed by incubation temperature, indicating that with sufficient burial time, seeds of this species germinated readily under appropriate thermal conditions. Soil moisture had a minor effect, while soil temperature had no significant influence on germination.

In *S. nigrum*, burial time remained dominant, but soil moisture and soil temperature notably also contributed to germination responses. Also, in *S. nigrum*, incubation temperature played no role at all as opposed to *A. blitoides*, and was the only species where it played no role. In *P. aviculare*, burial time continued to play a significant role, with soil moisture exerting a more pronounced effect than in *S. nigrum*, and incubation temperature also emerging as an important contributor. Following this, soil temperature was identified as the next significant factor. For *E. crus-galli*, burial time was dominant, but the effect of incubation temperature was even more prominent, with soil moisture again playing a tertiary role after incubation temperature as a secondary one. In contrast, *D. fusca* exhibited a distinct pattern: incubation temperature was the most critical determinant of germination, followed by burial duration and soil moisture (Figure 3b).

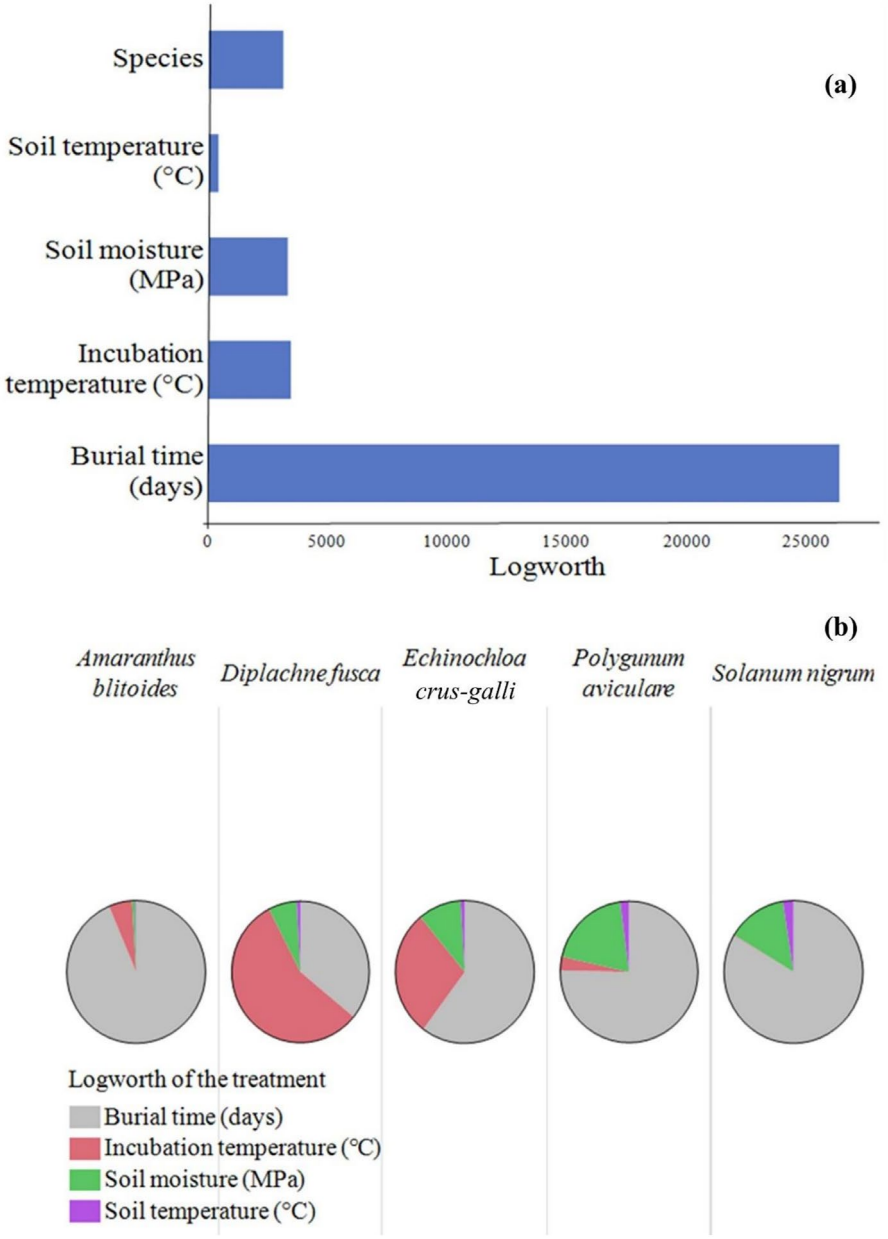


FIGURE 3 | Effects of experimental treatments on germination fractions, based on log-worth values calculated using the response screening method: (a) overall effects of treatments and (b) their relative importance for the five study species.

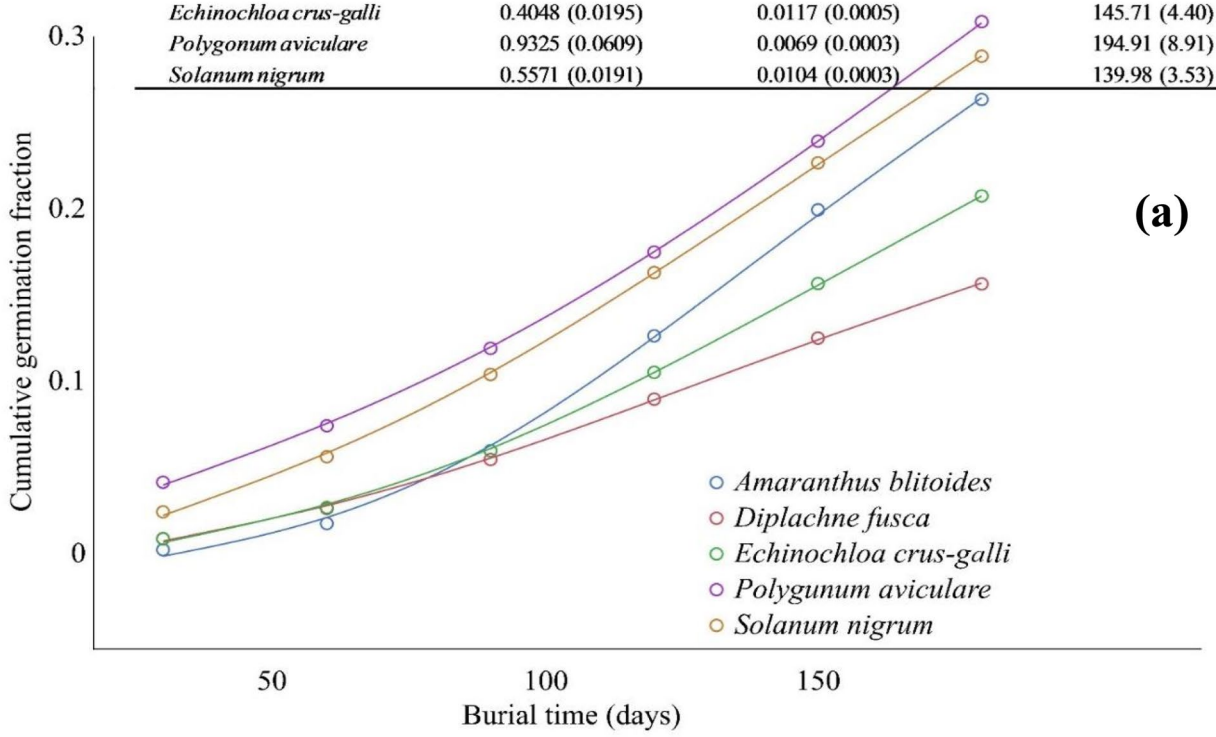
3.2 | Germination Changes Over Burial Time

Germination fractions of all five species, *A. blitoides*, *D. fusca*, *E. crus-galli*, *P. aviculare* and *S. nigrum*, increased with burial duration, following a sigmoidal trend indicative of gradual dormancy loss (Figure 4a). *Solanum nigrum* and *P. aviculare* exhibited significantly higher germination fractions at earlier burial durations ($p < 0.05$), indicating faster dormancy release, while *A. blitoides* and *D. fusca* showed lower germination fractions initially ($p < 0.05$), reflecting greater dormancy persistence. Despite species-specific differences, burial duration was the primary driver of dormancy release and germination response across all species ($p < 0.001$).

3.3 | Soil Temperature and Moisture Influence on Germination Fractions

Soil water potential had a significant positive linear effect on germination fractions across all species ($p < 0.01$), with slopes varying by species and soil temperature (Figure 4b). The slopes of germination fraction response to soil water potential at 2°C, 5°C and 8°C were, respectively: *A. blitoides* (0.014, 0.018, 0.020), *D. fusca* (0.038, 0.058, 0.064), *E. crus-galli* (0.040, 0.060, 0.070), *P. aviculare* (0.080, 0.100, 0.120) and *S. nigrum* (0.060, 0.080, 0.100). Statistical comparison of slopes revealed that *P. aviculare* and *S. nigrum* had significantly steeper slopes than *A. blitoides* and *D. fusca* at all temperatures ($p < 0.05$), indicating a stronger

Species	G_{max} (Asymptote)	b_{BT} (Growth Rate)	BT_{50} (Inflection Point)
Amaranthus blitoides	0.4061 (0.0099)	0.0165 (0.0005)	129.50 (1.74)
Diplachne fusca	0.2480 (0.0105)	0.0132 (0.0006)	121.46 (3.70)
Echinochloa crus-galli	0.4048 (0.0195)	0.0117 (0.0005)	145.71 (4.40)
Polygonum aviculare	0.9325 (0.0609)	0.0069 (0.0003)	194.91 (8.91)
Solanum nigrum	0.5571 (0.0191)	0.0104 (0.0003)	139.98 (3.53)



Amaranthus blitoides *Diplachne fusca* *Echinochloa crus-galli* *Polygonum aviculare* *Solanum nigrum*

Species	Intercept (SE)	Slope (SE)	p-value
Amaranthus blitoides	0.1307 (0.0011)	0.0180 (0.0011)	<0.0001
Diplachne fusca	0.1265 (0.0011)	0.0539 (0.0011)	<0.0001
Echinochloa crus-galli	0.1443 (0.0011)	0.0566 (0.0011)	<0.0001
Polygonum aviculare	0.2501 (0.0011)	0.1008 (0.0011)	<0.0001
Solanum nigrum	0.2178 (0.0011)	0.0821 (0.0011)	<0.0001

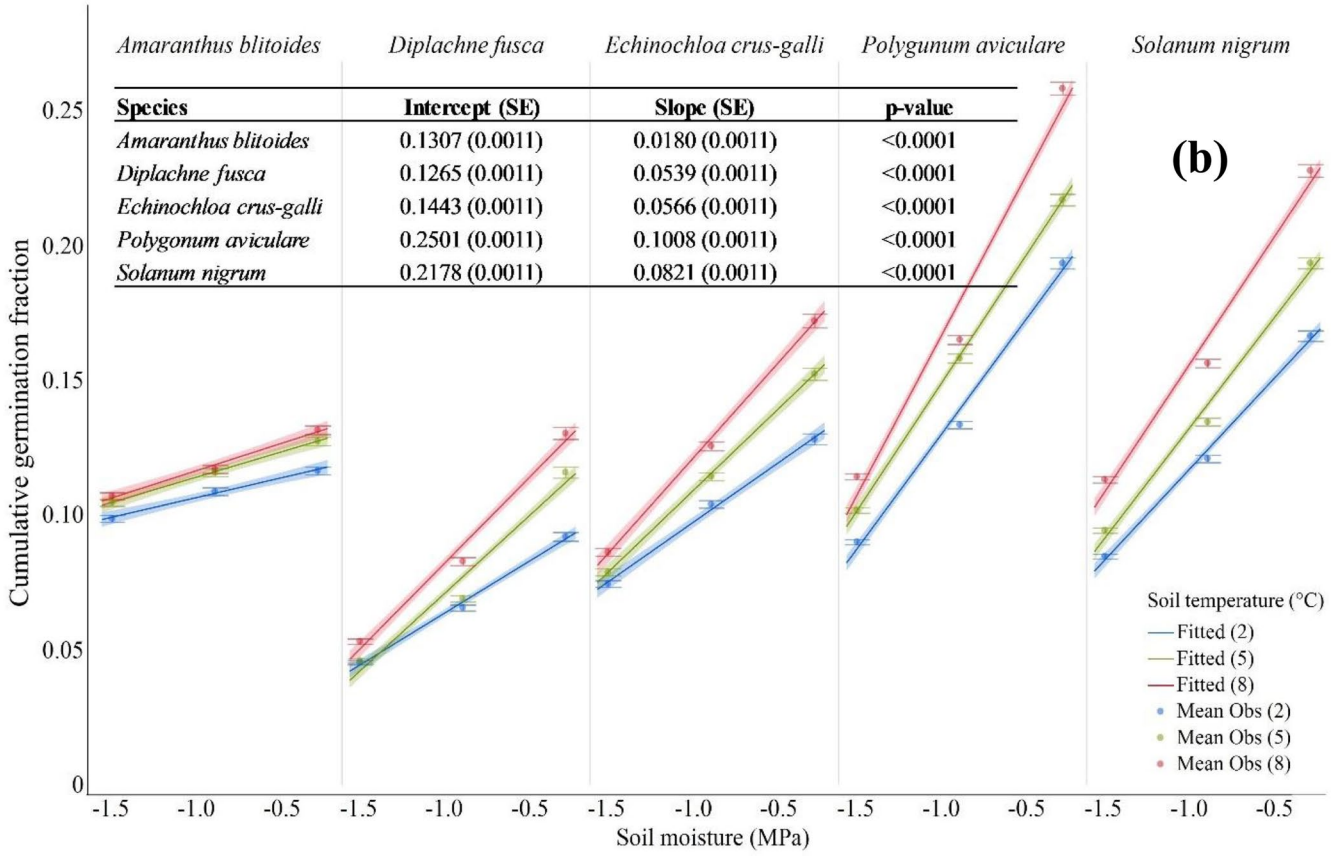


FIGURE 4 | (a) Sigmoidal increase in germination fractions over burial time. (b) Linear responses of germination fractions to varying soil moisture and temperature levels. Error bars indicate the standard error of the mean. Parameter estimates are presented with their standard errors in parentheses.

response to moisture. Higher soil temperatures significantly enhanced germination fractions in *D. fusca*, *E. crus-galli*, *P. aviculare* and *S. nigrum* ($p < 0.05$), with warmer conditions (8°C) yielding higher germination under equivalent moisture levels. In contrast, *A. blitoides* germination was insensitive to temperature changes ($p > 0.05$), showing no significant interaction with soil water potential.

3.4 | Changes in Base and Ceiling Temperatures With Dormancy Break Over Time

Response screening analysis (Figure 5a) confirmed burial period as the most significant factor influencing base temperature (T_b) and ceiling temperature (T_c) ($p < 0.001$), followed by soil moisture ($p < 0.05$). Soil temperature had no significant

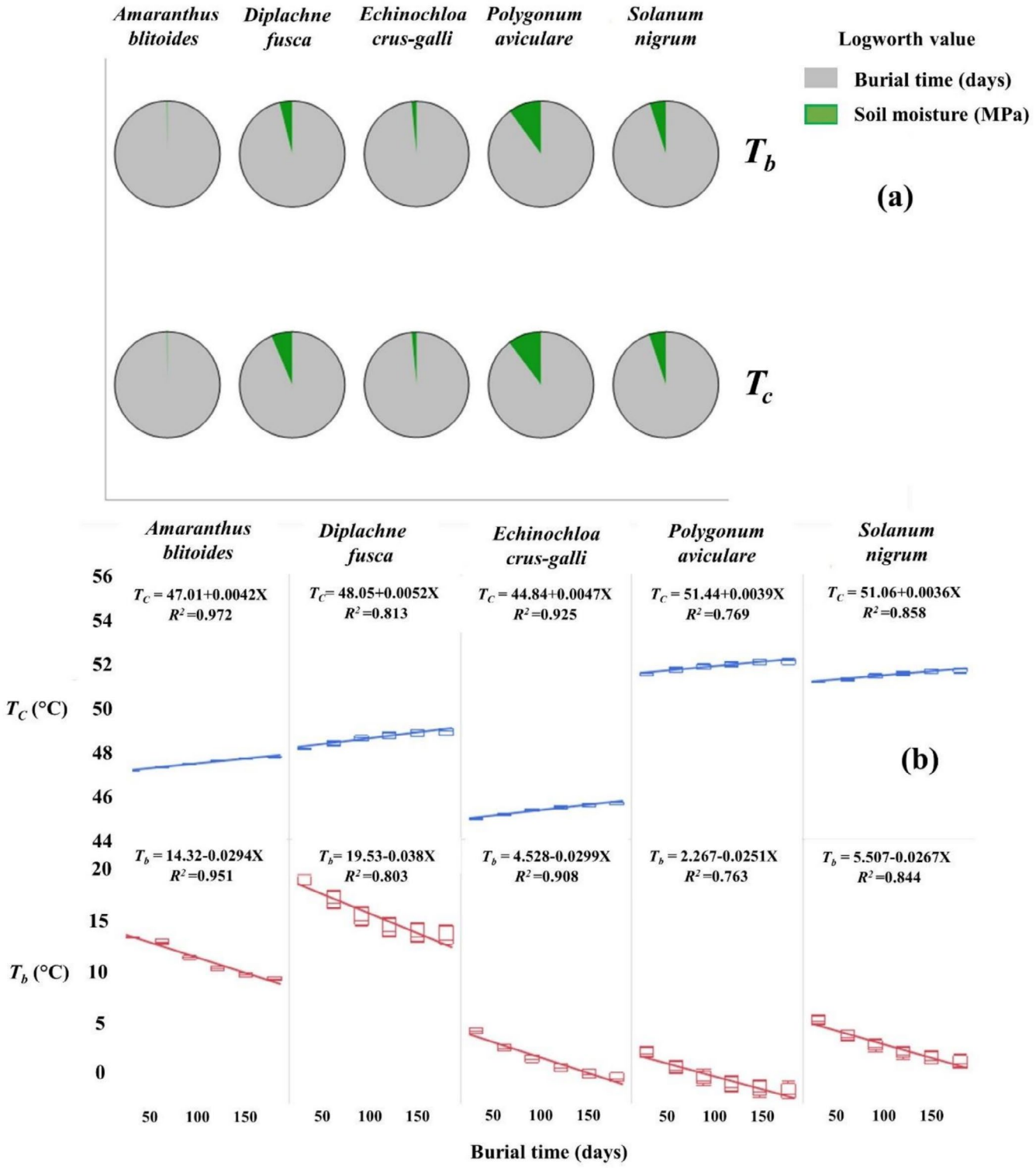


FIGURE 5 | (a) Relative influence of burial duration (grey) and soil moisture (green) on seed germination of five summer annuals, based on logworth values. Segment size reflects factor magnitude. (b) Changes in base (T_b) and ceiling (T_c) temperatures over burial time for each species.

effect on T_b or T_c ($p > 0.05$). For *A. blitoides*, burial period was the dominant factor ($p < 0.001$), with soil moisture showing negligible influence ($p > 0.05$). *Polygunum aviculare* exhibited the highest sensitivity to soil moisture ($p < 0.01$), followed by *S. nigrum* ($p < 0.05$). In *D. fusca*, T_c was more strongly affected by soil moisture than T_b ($p < 0.05$). As shown in Figure 5b, T_c increased modestly with burial time across most species, with the highest rates in *D. fusca* (slope = 0.0052, $p < 0.05$) and *E. crus-galli* (slope = 0.0047, $p < 0.05$). T_b decreased significantly with burial duration, particularly in *D. fusca* ($p < 0.01$), *E. crus-galli* ($p < 0.01$) and *A. blitoides* ($p < 0.05$), indicating a stronger adjustment in the base temperature threshold as dormancy was alleviated.

3.5 | Thermal Time Accumulation During Burial

Cumulative thermal time increased significantly with burial duration for all species across all soil moisture levels and temperature treatments ($p < 0.001$; Figure 6). *Amaranthus blitoides* exhibited the highest cumulative thermal time, followed by *D. fusca*, *E. crus-galli*, *P. aviculare* and *S. nigrum* ($p < 0.05$ for interspecies differences). Higher soil moisture significantly increased thermal time within each burial duration ($p < 0.01$), with the effect being more pronounced at 5°C and 8°C than at 2°C ($p < 0.05$). The slopes of thermal time increase with soil moisture were steepest in *E. crus-galli*, *P. aviculare* and *S. nigrum* ($p < 0.01$), particularly at longer burial durations (≥ 90 days). At shorter burial durations (30 and 60 days), differences in thermal time across soil temperatures were not significant ($p > 0.05$), but at longer durations (≥ 90 days), thermal time at 8°C was significantly higher than at 2°C and 5°C under similar moisture conditions ($p < 0.05$).

3.6 | Predicting Germination Fractions

The cumulative germination fraction (*CGF*) under varying environmental conditions was successfully modelled using the Weibull function (Equation 12). The model incorporated key

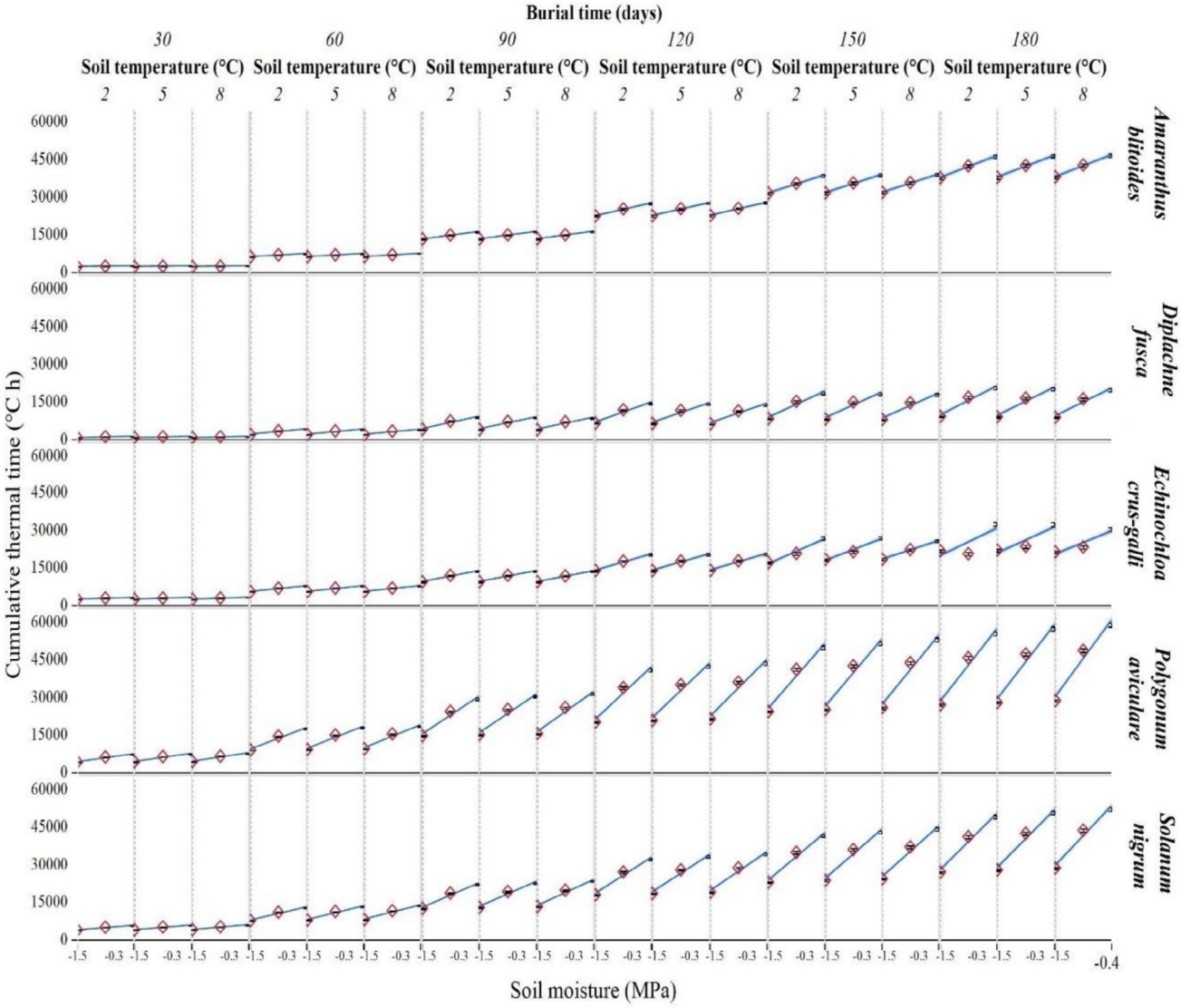


FIGURE 6 | Thermal time accumulation (represented by the area of triangles) by seeds under various combinations of soil temperature, moisture and burial periods within the range of experimental germination temperatures.

factors influencing dormancy and germination, including soil moisture, temperature, burial duration and the subsequent incubation temperature and time. The predictive performance of the model was rigorously evaluated through a one-to-one comparison of observed versus predicted germination fractions, as visually summarised in Figure 7. The scatter plots in this figure demonstrate a strong agreement between the modelled output and the empirical data across all species investigated. Quantitative analysis of the model's accuracy was conducted using the root mean square error (*RMSE*) and the coefficient of determination (R^2). The *RMSE* values were consistently low, indicating a high level of precision. Specifically, the model was most accurate for *A. blitoides* (*RMSE* = 0.04), followed by *E. crus-galli* (*RMSE* = 0.07). Furthermore, the goodness-of-fit, as measured by R^2 values, confirmed the model's robustness in explaining the variation in the germination data. The model accounted for a substantial proportion of the observed variance, with R^2 values ranging from 0.817 for *E. crus-galli* to 0.911 for *A. blitoides*. This indicates that the Weibull model explained over 81% of the germination variability for all species, with the highest explanatory power (91.1%) demonstrated for *A. blitoides*.

3.7 | Inter-Species Variation in Germination Thermal Parameters

Parameter estimates (Table 1) showed that the base temperature (T_b) at which germination begins varied among species. *P. aviculare* and *E. crus-galli* had the lowest T_b values of 4.10°C and 5.70°C, respectively, indicating germination can start at cooler temperatures. In contrast, *D. fusca* required a higher T_b of 19.68°C, suggesting it initiates germination only under warmer conditions. The optimum temperature range, defined by lower (T_{O1}) and upper (T_{O2}) limits, also varied. *E. crus-galli* exhibited a broad range from 19.88°C to 33.19°C, while *P. aviculare* showed a narrower range between 14.09°C and 27.29°C. *Solanum nigrum* had the highest T_{O1} value at 25.99°C, indicating a higher threshold for optimum germination. The ceiling temperature (T_c), representing the maximum temperature for germination, was highest for *P. aviculare* (49.58°C) and *S. nigrum* (49.32°C) and lowest for *E. crus-galli* (43.10°C), reflecting species-specific thermal tolerance limits. Burial time at which 50% of maximum germination is reached (BT_{50}) varied, with *E. crus-galli* showing the longest BT_{50} of 198.14 days, suggesting a

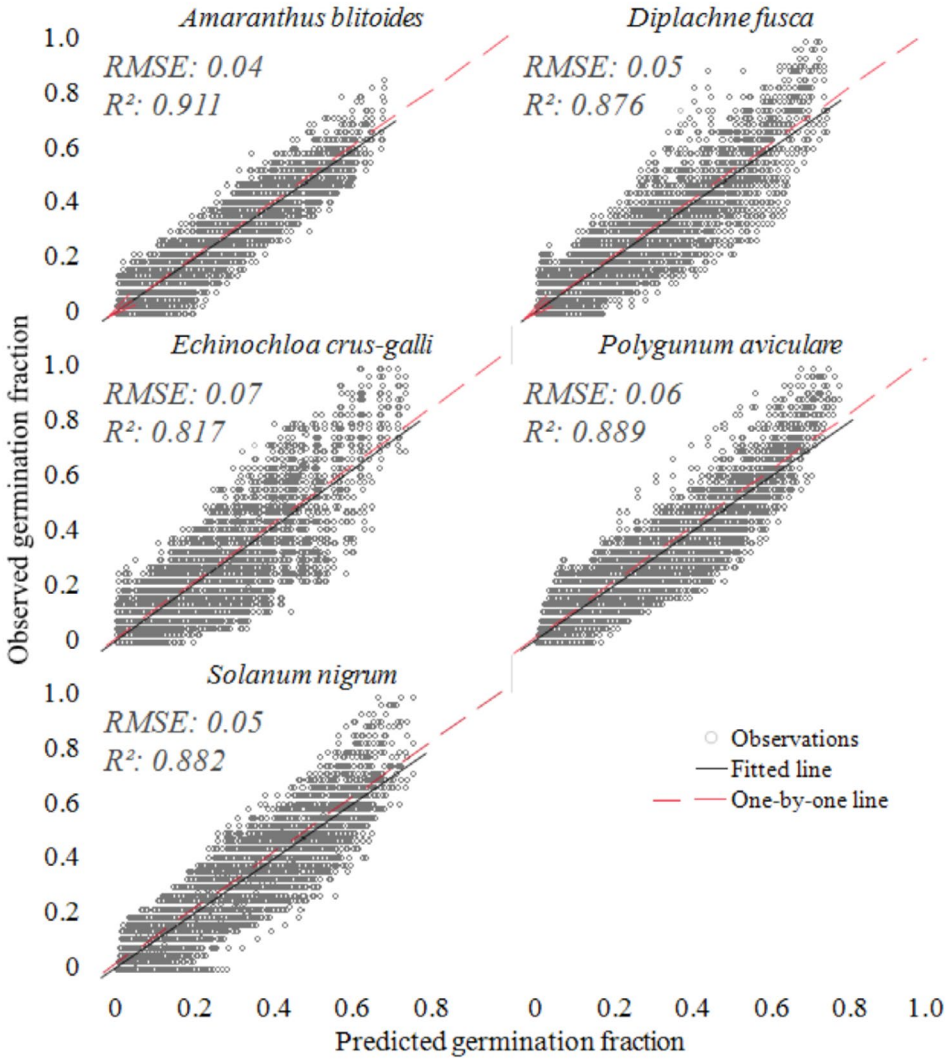


FIGURE 7 | One-to-one lines compare observed germination fractions with predictions from Equation (12), fitted separately for each species using their species-specific parameters (Table 1). Model performance is shown by R^2, *RMSE* and *MBE*.

slower dormancy break. Conversely, *D. fusca* had the shortest BT_{50} at 140.19 days, indicating more rapid dormancy release.

Figure 8 summarises the simulated germination fractions of the five species under varying soil temperatures and moisture levels. Cumulative germination fractions were generally higher at 8°C than at 2°C across most species. The difference between the two soil temperatures was minor after 30 days of burial but became increasingly evident after 120 and particularly 180 days. At 8°C, germination increased substantially in *A. blitoides* and *D. fusca* under both moisture levels, while *S. nigrum* and *P. aviculare* exhibited moderate enhancement. In contrast, *E. crus-galli* showed minimal sensitivity to soil temperature across treatments. The positive effect of 8°C was most evident under higher soil moisture (−0.3 MPa), whereas temperature effects were negligible at −1.5 MPa. Overall, prolonged burial under moist conditions followed by exposure to 8°C consistently promoted greater cumulative germination than at 2°C.

4 | Discussion

4.1 | Response to Temperature and Moisture During Burial

Seeds buried at higher soil temperatures, particularly at 8°C, accumulated greater thermal time (TT) compared with seeds buried at 2°C, indicating faster progression toward germination. In *A. blitoides*, soil temperature during burial had no detectable effect, suggesting species-specific temperature sensitivity. These findings are consistent with Baskin and Baskin (2022), who reported that even under warmer winter conditions, sufficient cold days remain to fulfil stratification requirements for breaking dormancy in summer annuals.

The soil burial period was identified as a critical factor controlling dormancy break and germination (Figure 2a). Extended burial allowed seeds to accumulate sufficient exposure to low temperatures, fulfilling their cold stratification requirement and thereby promoting dormancy release. Similar patterns have been reported by Kępczyński and Sznigir (2013), who observed that prolonged burial mitigates seed sensitivity to cold stratification.

Soil moisture also played a central role in germination. Higher moisture availability (−0.3 MPa) enhanced TT accumulation and accelerated germination relative to drier conditions (−1.5 MPa), reflecting its importance in seed imbibition, the initial step in germination that activates key enzymes and biochemical pathways (Cheong and Lim 2023). Moist soils buffer against temperature fluctuations, stabilise environmental conditions (Khaeim et al. 2022) and enhance temperature effects on germination by maintaining consistent hydration. In drought-sensitive species such as *P. aviculare* and *S. nigrum*, soil moisture exerted a stronger influence than incubation temperature, indicating that hydration is a primary driver of dormancy break (Figure 2b). Although hormonal

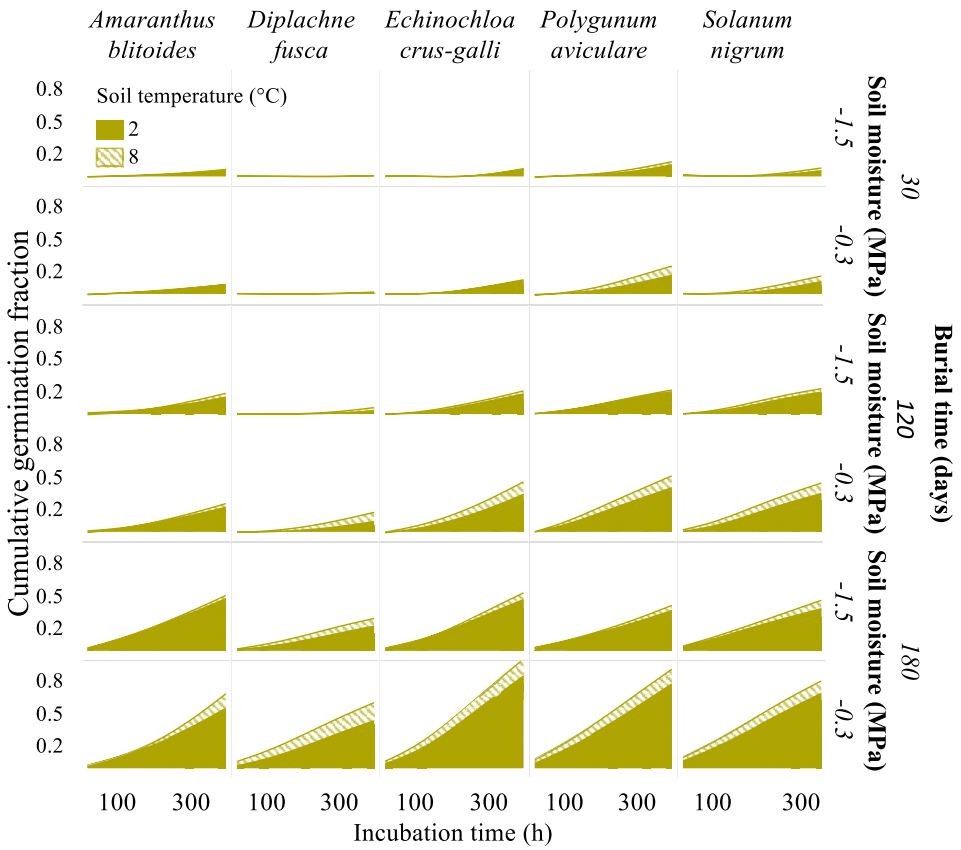


FIGURE 8 | Cumulative germination fractions of five summer annual species over incubation time under different burial durations (30, 105 and 180 days), soil moisture levels (−1.5 and −0.3 MPa) and soil temperatures (2°C, solid fill; 8°C, hatched fill). Each panel illustrates the interactive effects of burial environment and subsequent germination conditions, highlighting species-specific patterns of dormancy release and germination sensitivity to soil temperature and moisture. The hatched area denotes the enhancement in cumulative germination at 8°C relative to 2°C.

changes were not measured, these results are consistent with the reported effects of moisture on ABA and GA levels, which regulate dormancy and promote germination (Hu et al. 2018; Lewandrowski et al. 2017).

4.2 | Pronounced Shifts in Base Temperature (T_b) Versus Minimal Changes in Ceiling Temperature (T_c)

Base temperature (T_b) was more responsive than ceiling temperature (T_c), reflecting distinct physiological roles in germination. Across species, T_b decreased with prolonged burial and adequate moisture, indicating increased sensitivity to cooler conditions and flexible adjustment of germination timing. T_c remained relatively stable, acting as a thermal safeguard that prevents germination under potentially damaging high temperatures. These patterns support the conceptual framework of Baskin and Baskin (2022) and Bradford and Bello (2022), in which T_b functions as a flexible 'environmental window' while T_c serves as a rigid protective threshold.

Burial duration was identified as the predominant factor controlling both T_b and T_c, highlighting the importance of extended soil residence in dormancy cycling. Prolonged burial exposes seeds to sustained darkness and hypoxic conditions, which suppress metabolic activity and promote adaptive shifts in germination thresholds, thereby preventing emergence under ecologically unfavourable periods (Finch-Savage and Footitt 2017; Long et al. 2015). Soil moisture influenced germination thresholds to a lesser extent, primarily by governing imbibition rates and water potential gradients essential for metabolic reactivation, without fundamentally redefining the thermal range for germination (Batlla and Benech-Arnold 2014). Soil temperature had the least impact on germination thresholds, likely due to its transient variability and lower selective pressure compared with consistent cues from burial duration (Saatkamp et al. 2011; Bradford and Bello 2022). The intermediate role of soil moisture likely reflects its dual function as a physiological trigger for metabolic activity and as a modulator of dormancy release.

4.3 | Predicting Climate Change Impact

Amaranthus blitoides is predicted to maintain stable dormancy-break and germination potential under warmer and drier conditions, suggesting minimal risk of delayed germination or disruption in its regeneration cycle (Talaee et al. 2024). *Diplachne fusca* is expected to exhibit accelerated dormancy-break and faster germination with warmer winters and adequate soil moisture; although drought conditions may limit this response (Song et al. 2024). *E. crus-galli* is likely to benefit from warmer burial conditions provided that moisture availability is sufficient; however, dry conditions may constrain temperature-driven dormancy break, consistent with observations by Royo-Esnal et al. (2022). *Polygunum aviculare* may experience enhanced dormancy-break under climate warming, but this is dependent on adequate soil moisture and insufficient water may delay germination due to maintained dormancy (Malavert et al. 2020). *S. nigrum* is predicted to benefit from warmer winter soil conditions if moisture is not limiting, but drought-prone environments could suppress germination (Ma et al. 2021).

Although seeds were collected from multiple mother plants and pooled to account for genetic variation and to minimise maternal effects (Donohue 2009), the study relied on a single population per species. Consequently, population-specific genetic and environmental factors may have influenced germination responses (Bischoff and Müller-Schärer 2010). Therefore, the results should be interpreted as representative of these populations rather than species-wide responses. Nonetheless, the observed patterns provide mechanistic insights into how soil temperature, moisture and burial duration interact to regulate dormancy and germination under changing climatic conditions.

5 | Conclusion

Based on our results, species such as *A. blitoides*, which show low sensitivity to soil temperature and moisture during burial, are unlikely to exhibit substantial shifts in germination behaviour under future climate conditions. In contrast, *D. fusca*, *E. crus-galli* and *S. nigrum* may display an increased potential for dormancy break under warmer winter soil temperatures, although this response is likely to remain strongly dependent on adequate soil moisture during burial. While prolonged burial could partially compensate for species-specific thermal and moisture requirements, its influence is expected to interact with these factors in a complex manner. Overall, our findings indicate that earlier seedling emergence may occur under warmer and sufficiently moist winter conditions, though the extent of this response will vary among species. Future research should include multiple populations to better capture intraspecific variability and elucidate how genetic differentiation interacts with environmental conditions to shape species-specific responses.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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