Review

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Review

Developing Population-Based Threshold Models for Predicting Weed Emergence in Time and Space to be Used in Site-Specific Weed Management

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Abstract

Effective weed management is crucial for optimizing agricultural productivity and minimizing environmental impacts. Weeds are most effectively managed during their seedling or early growth stages, something that could be efficiently achieved with the aid of tools for predicting seedling emergence. However, many persistent weed species exhibit dormant seedbanks thus complicating prediction attempts. The number of emerged seedlings in these species is closely tied to seedbank dormancy levels, which are influenced by seasonal variations. Thus, predictive population-based threshold models incorporate seedbank dormancy regulation to accurately forecast seedling "window" emergence. These models use the functional relationship between environmental cues (i.e., temperature, light, alternating temperatures, and soil water content) and seed dormancy behavior. Considering that these environmental signals vary among microsites in the field, these tools can be adapted to predict weed emergence in both temporal and spatial dimensions, thus making them suitable for site-specific weed management. The aim of this paper is to provide a framework for dynamic, site-specific weed emergence predictions, enabling targeted weed management practices. This kind of approach can help to improve the efficiency of herbicide applications and other control measures, reducing costs and environmental impact while enhancing crop yields. This work underscores the potential of integrating environmental cues into sophisticated modeling approaches to address the complexities of weed emergence in diverse agricultural landscapes.

Keywords: germination; seed dormancy; weed emergence; population-based threshold models; sustainable agriculture

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1. Introduction

The incidence of weeds in agronomic crops causes significant reductions in the profitability of agricultural production systems [1]. On the one hand, weeds compete with arable plants for soil nutrients, water, and light [2–5]. On the other hand, they can affect harvesting operations, the quality of harvested grain, and serve as a source of insects and diseases harmful to crops [6]. Understanding these negative aspects is essential because it allows for the development of targeted and efficient weed control strategies, reducing the negative impacts on crop yields and quality. Furthermore, it aids in the optimization of resource use, minimizing the environmental footprint of agricultural practices.

In the last decades, control strategies were mainly based on the use of herbicides, particularly glyphosate [7–9]. However, the reduced availability of products to selectively control weeds, the increase in the frequency of individuals resistant and tolerant to the application of certain herbicides, as well as the growing pressure to reduce the use of agrochemicals due to their harmful effects on the environment, make it necessary to optimize the application of control measures within a framework of more rational control strategies [10]. Despite the progress made in understanding the key processes of weeding - such as dispersal, competition, and establishment of weeds - in recent decades, the persistence of the problem in current agricultural systems highlights our inability to predict and control this phenomenon with sufficient precision [11]. This is partly due to our lack of knowledge regarding various aspects related to the regulation of weeding processes [3,12]. However, the possibility of designing more effective integrated weed management systems depends not only on gathering this knowledge, but also on the ability to predict in time and space, and under different environmental and management practice scenarios, the intensity with which the weeding processes occur [11,12]. In this sense, predicting weed emergence is of vital importance, as the seedling stage is the most vulnerable to control practices [13,14]. To achieve this, it is necessary to understand different aspects of weed biology underlying the emergence process, such as dormancy and germination, as a preliminary step to develop tools to guide decision-making [4,12,15,16]. Although there is a wealth of published information related to the study of these biological aspects in many weedy species of agricultural importance, this knowledge is scattered and not enough efforts have been made to integrate this information within a conceptual framework that would allow the development of transfer tools to assist farmers and technicians in decision-making for the management of weeds under both productive and environmental rationales.

Weed management is a critical aspect of agricultural practices, significantly impacting crop yields and environmental sustainability. However, predicting the timing of weed emergence is challenging due to seed dormancy and the formation of persistent seedbanks. By integrating germination and dormancy models with site-specific weed management, growers can tailor control strategies to local conditions, improving the timing and precision of interventions. This approach enhances the effectiveness of weed control by addressing the unique dynamics of seedbanks in specific fields.

2. Seed Dormancy in Weed Species

Seed dormancy is a critical factor in the persistence of weed seedbanks and the timing of weed emergence [17]. Dormancy mechanisms allow weed seeds to remain ungerminated in the soil for extended periods, emerging when conditions are favorable [18]. The regulation of dormancy is influenced by various environmental cues, including temperature, light, alternating temperatures, and seed water content [19,20]. Understanding these cues and their interactions is essential for developing models that can predict weed emergence accurately. Seed dormancy is possibly the process that most affects seedbank emergence dynamics in agricultural fields [4,12], and it can be caused by one or more blockages which result in the failure to germinate even under adequate moisture, aeration, and temperature conditions [3,21–24].

In an attempt to formulate a definition, Bewley and Black [25] define dormancy as an internal characteristic of the seed that prevents germination under environmental conditions that would otherwise have been suitable for germination. On the other hand, Vleeshouwers et al. [26], stated that dormancy is “a characteristic of the seed, the level of which will define what conditions must be met for the seed to germinate”. Later, Benech-Arnold et al. [3] proposed a definition of dormancy that reinforces the intrinsic character of the phenomenon, defining it as “an internal seed condition that prevents seed germination under water, thermal and gaseous conditions that would otherwise have been suitable for germination to take place”. All these definitions denote that once the impedances have been removed, germination will occur under a wide range of environmental conditions. Depending on the timing of dormancy, dormancy can be classified into primary and secondary dormancy [24,27]. Primary dormancy refers to the dormancy of seeds dispersed from the mother plant, while secondary dormancy results from the reinduction of dormancy in seeds that had been previously released from primary dormancy [27–31].

In many cases, release from primary dormancy is followed by subsequent reinductions into secondary dormancy, determining the existence of cyclical patterns in the dormancy level (Figure 1).

Many problematic weeds, particularly those capable of forming persistent seed banks, often exhibit cyclical changes in dormancy [32]. For example, many spring annuals have a high dormancy level in autumn after dispersal, which decreases during the cold winter months and then increases again in the summer months. In contrast, winter annual species generally show an inverse temporal pattern in their dormancy level changes [33]. This behavior highlights the adaptive value of dormancy, which plays an important role in the adaptation of plants to their environment, allowing them to identify the season of the year with favorable environmental conditions for plant establishment and constraints for establishment as the presence of a dense canopy or burial at depths from where a seedling cannot emerge [24,34].

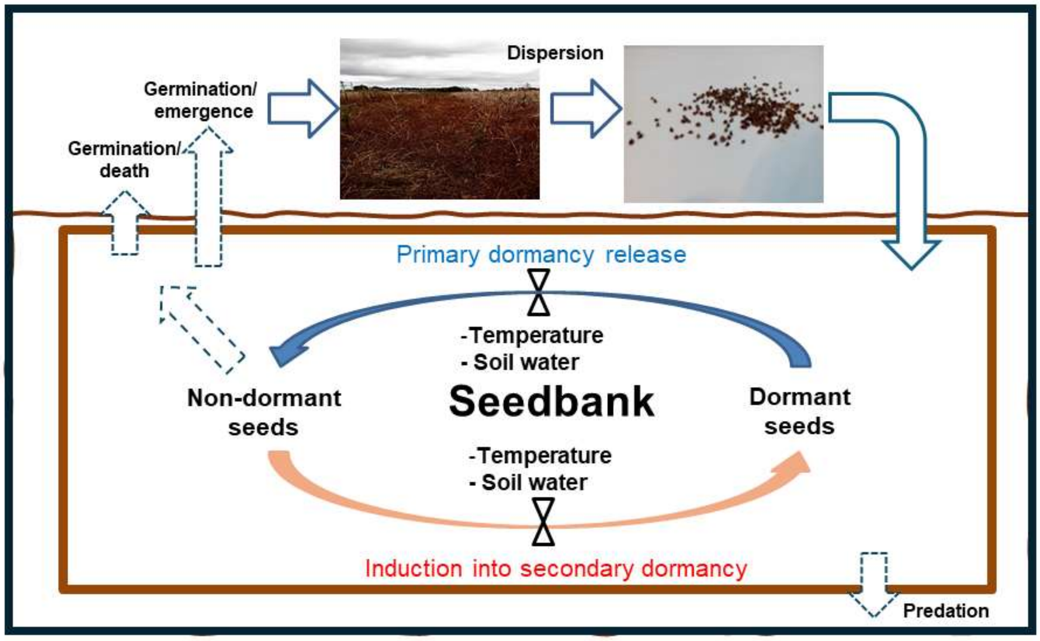

Figure 1. Schematic representation of seedbank dynamics for weed species with seed dormancy. Dotted arrows and dashed lines represent seed outputs (i.e., predation, germination/death, germination/emergence), solid arrows represent seed inputs. Blue and orange arrows represent cyclic changes between dormant and non-dormant seeds.

3. Environmental Factors Regulating Changes in Seed Dormancy

The main environmental factors regulating weed emergence patterns are temperature and water availability [35,36]). These factors alter the dormancy level of seed banks determining seasonal patterns of weed emergence in the field [19]. In winter annual species, high summer temperatures act as dormancy relievers, while low winter temperatures induce induction into secondary dormancy of seeds [24]. This is the case for *Capsela bursa-pastoris* [37], *Avena fatua* [38], *Lolium rigidum* [39], *Bromus tectorum* [40] and *Lithospermun arvense* [41] and many others. In contrast, in summer annuals, the low temperatures experienced during winter act as dormancy relievers determining a minimum dormancy in early spring, while the high temperatures that prevails in late spring/early summer, produce an increase in the dormancy level determining through entrance into secondary dormancy; this is the case of *Chenopodium album* L., *Sysimbrium officinale* L., *Polygonum persicaria* L. [42], *Polygonum aviculare* L. [14,43,44], *Ambrosia artemiisifolia* L. [45], *Echinochloa crus-galli* [46] and many others.

The process by which summer annual species are released from dormancy during winter is known as 'stratification' or 'chilling', and is equivalent to expose the seeds to low temperatures under humid conditions. In the case of winter annuals, high summer temperatures acting on seeds with a low moisture content, alleviate dormancy; this process is called 'after-ripening'. The moisture content of the seeds determines whether or not the above-mentioned processes (i.e., stratification or after-ripening) take place, as the moisture content of the seeds acts as a modulator of the effect of temperature on the dormancy level [20,47]. For example, Wang et al. [48] observed that dormancy release at low temperatures in *Vitis vinifera* was zero below 20% seed moisture and then increased to a maximum at 40% seed moisture. In turn, Bair et al. [36] quantified the effect of soil water status on the dormancy release in seeds of *B. tectorum*, observing that the inclusion of this factor in the model developed improved the prediction made. More recently, Malavert et al. [20] quantitatively characterized the interaction between seed water content (SWC) and stratification temperature. The authors observed that in *P. aviculare* seeds, the dormancy release rate was zero below 15% SWC and above that value, the release rate increased until it became maximal at 31% SWC. These results made it possible to describe the modulating effect of SWC on changes in dormancy level and to test a model that predicts adequately changes in *P. aviculare* dormancy level as a function of the variation in SWC experienced by the seeds in the soil. Beyond this evidence, very few studies have attempted to quantify the effect of soil water content on seed moisture content and how this affects the cyclical changes in the dormancy level of seed populations.

Seed dormancy is a relative rather than an absolute phenomenon. The concept of relative dormancy levels was introduced by Vegis [49] from observations obtained during the dormancy release process: the range of temperatures permissive for germination widens to a maximum as seeds are released from dormancy. In contrast, as dormancy is induced, the range of temperatures within which germination can proceed narrows until germination is no longer possible at any temperature. On this basis, Karssen [24] proposed that seasonal patterns of emergence of annual species are the combined result of seasonal cycles in soil temperatures and physiological changes within seeds that alter the permissive temperature range for germination. Therefore, germination in the field is restricted to periods when soil temperature and the temperature range within which germination can proceed overlap (Figure 2).

Thus, an increase or decrease in the dormancy level could be expressed as a widening or narrowing of the permissive temperature range for germination. These variations in the range of permissive temperatures for germination can be quantified from two threshold limit temperatures: lower limit temperature (T_l) and higher limit temperature (T_h) [14,43,50]. These threshold temperatures (T_l and T_h) vary among seeds within the same population [14,43,50]. For example, $T_{l(50)}$ and $T_{h(50)}$ represent the temperatures below and above which dormancy is expressed for 50% of the population. In summer annuals, changes in the dormancy level are due to increases or decreases in T_l, while in winter species are due to fluctuations in T_h. For summer annual species, such as *P. aviculare*, germination of a fraction of the seedbank population occurs when the increase in soil temperature (in spring) exceeds the T_l for that fraction [26,44,51]. This proportion of the seedbank able to emerge at a given time can be predicted if the distribution of T_l within the seed population and its associated changes with the level of seed dormancy, are known [33,43,44], see Figure 2.

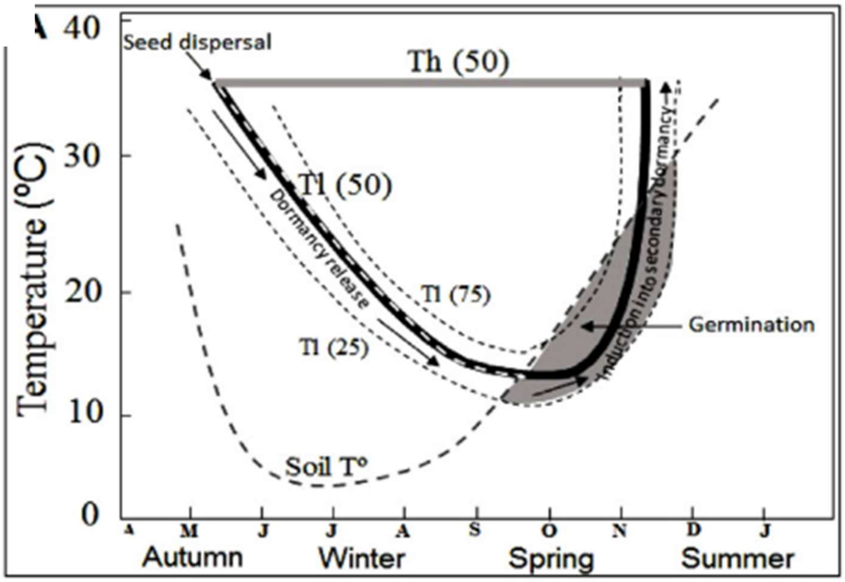

Figure 2. Schematic representation of seasonal changes in the permissive germination thermal range and its relationship with soil temperature dynamics for *Polygonum aviculare* seeds. Solid black lines indicate the mean lower ($T_{l(50)}$) and grey solid line the mean higher ($T_{h(50)}$) limits temperatures of the permissive thermal range allowing germination. Dashed black lines indicate T_l for the 25 and 75 seed population percentiles. Dashed gray line indicates the soil temperature (soil Tº). The gray zone represents the moment when germination occurs once the soil temperature enters in the permissive thermal range. Black arrows indicate the lowering and increase in T_l during dormancy release and induction, respectively (originally from Probert [52], adapted from Malavert et al. [44]. .

4. Seed Dormancy Terminating Factors

As previously mentioned, the dormancy level is constantly changing in the seedbank. Often, when the dormancy level of a seed population is sufficiently low, certain species require exposure to specific environmental signals that act as dormancy terminators. These signals remove the final barriers and initiate the germination process [3,53,54]. Among the most studied dormancy-terminating factors are light and alternating temperatures, as these typically have the greatest effect under field conditions [55–58]. The requirement for light is associated with the possibility of detecting gaps in the canopy or the depth to which the seeds are buried and is also regarded as an adaptation to recurrent tillage operations in agricultural systems [3,53]. Conversely, alternating temperatures constitute an important environmental signal for dormancy termination, since below the first millimeters of depth in the soil, the influence of the light environment is null and, therefore, alternating temperatures are the only way of detecting burial depth [59–61].

The changes in dormancy level not only comprise changes in the range of temperatures permissive for germination, but also changes in the sensitivity of the seed population to the effects of these dormancy-terminating factors [3]. For example, in the case of seeds that require light stimulus to terminate dormancy, Batlla and Benech-Arnold [56] and Malavert et al. [57] observed that the dynamics of changes in the dormancy level in *P. aviculare* seeds during stratification were associated with changes in the light sensitivity of the seed population: sensitivity increased as dormancy decreased and *viceversa*. Similarly, for seeds requiring temperature fluctuations to terminate dormancy, Benech-Arnold et al. [62] showed that the size of the fraction in *Sorghum halepense* L. seed population responding to the stimulatory effect of temperature fluctuations increased as a consequence of a burial period under winter temperatures. The authors observed that this increase was also accompanied by changes in the number and amplitude of fluctuating temperature cycles required to complete exit from dormancy. *S. halepense* seeds that had spent one winter buried in the soil required exposure to fewer cycles of alternating temperatures to exit from dormancy and acquired the ability to respond to cycles of lower thermal amplitude.

5. Population-Based Threshold Models

The use of predictive models in weed control strategies is becoming increasingly relevant due to current pressures to reduce the excessive use of chemical controls in agricultural production [46,63]. These models rely on biological timing, where germination occurs at different rates depending on environmental conditions [64,65]). These rates are determined by the progress towards germination as a function of the difference between environmental conditions and a minimum threshold value, below which germination does not occur, or a maximum threshold value, above which there is also no response [1966]. For example, the timing and likelihood of seed germination are determined by the seed’s threshold sensitivity to environmental signals - the greater the signal above the threshold, the faster the response.

Population-based threshold models (PBTMs) describe how individuals within a population respond to environmental factors based on varying thresholds. In these models, each individual has a specific threshold for responding to cues like temperature or moisture, leading to a diversity of responses across the population [66]. As environmental conditions change, more individuals surpass their thresholds, resulting in cumulative population-level responses, often represented as quantal outcomes (i.e., germinated or not) [67,68]. PBTMs are useful for predicting collective behaviors in populations, such as seed germination patterns or emergence timing, by accounting for individual variation within a population. This kind of approach can be a robust tool for predicting how weed populations respond to environmental shifts, making them increasingly relevant in adapting weed control strategies to the impacts of global climate change. Some of the most used PBTMs consider germination in the predictions; however, very few models consider changes in dormancy level in their predictions. The most common germination models are:

6. Models to Predict Germination:

Thermal time model (TT): This model predicts germination in non-dormant seeds as a function of soil temperature. This type of model consists of certain variables that need to be characterized to estimate the percentage of seed population germination at a given time: base temperature (T_b), optimum temperature (T_o), maximum temperature (T_m), and thermal time (TT) required for a specific fraction of the population to germinate (i.e., 25% (TT_{25}), 50% (TT_{50}), and 75% (TT_{75}) of the population). The model accumulates degree days (ºCd) per day from a T_b in a sub-optimal (i.e., $T_b > T_o$) and supra-optimal ($T_o > T_m$) temperature range (Figure 3a). It is useful for studying germination at different temperatures (a wide range of temperatures). This approach has been applied to species such as *Setaria* (i.e., *S. viridis*, *S. verticillata*, and *S. glauca*; [69], and the work demonstrates that *S. glauca* has lower cardinal temperatures compared to other *Setaria* species. Using this model, the germination requirements and time of emergence can be predicted to optimize weed management for these species. In *Amaranthus retroflexus, Chenopodium álbum, Digitaria sanguinalis* and *Abutilon theophrasti* a similar approach was used to identify the T_b and TT to predict the cumulative emergence in the field [70]. This type of approach has been widely used to determine T_b and TT of many weeds which is critical for optimizing weed control timing, since knowing when a certain proportion of weed seeds will likely emerge enables precise application of herbicides or cultivation practices.

Hydrotime (HT) model: This model focuses exclusively on the effect of water potential (Ψ) on seed germination. It assumes that each seed within a population has a specific base water potential threshold for germination, which enables the modeling of population-level responses under varying levels of water availability (Figure 3b; [71]. The model has been successfully applied to quantify the effects of water potential on germination and to describe the variability in germination timing among individual seeds. For example, Huarte [72] applied the hydrotime model to several non-cultivated species, estimating key parameters such as the hydrotime constant (θ_H), the median base water potential ($\Psi_{b(50)}$), and its standard deviation ($\sigma_{\Psi b}$). This approach revealed that individual seeds differ in their base water potential thresholds, resulting in heterogeneous germination patterns across environmental conditions. Similarly, Tao et al. [73] applied the model to *Astragalus sinicus*, a forage legume, and demonstrated that hydrotime parameters not only vary between seed lots but also correlate with seed vigor and seedling emergence performance. In another example, Boddy et al. [68] used the hydrotime approach with *Echinochloa phyllopogon*, showing how environmental data combined with HT modeling can accurately describe temperature and moisture effects on germination and emergence, supporting improved weed control strategies. Collectively, these studies highlight the versatility and predictive value of the hydrotime model for understanding and managing seed germination under water-limited and fluctuating environmental conditions.

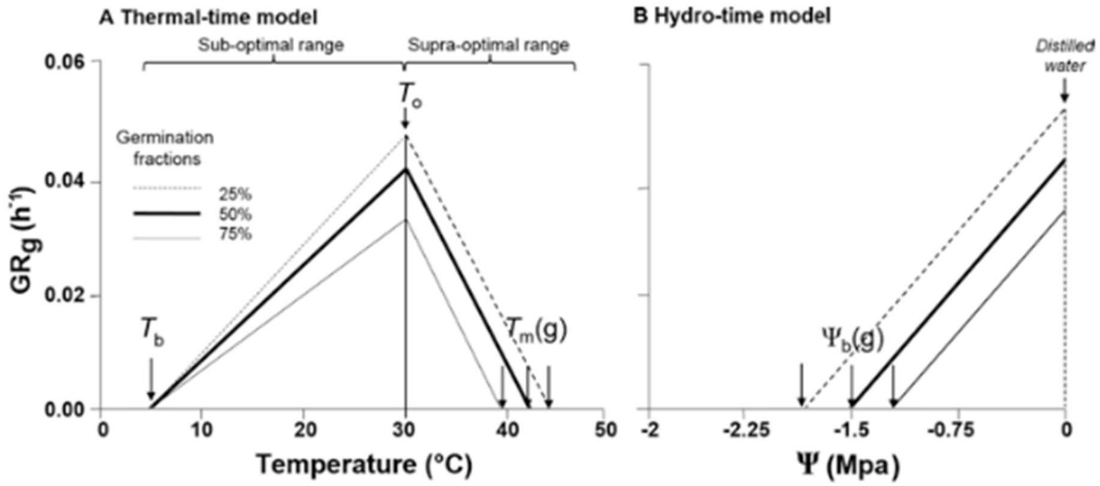

Figure 3. (A) Schematic representation of the relationship between germination rates (GRg= 1/tg) and temperature at the suboptimal and the supra-optimal thermal range for 25, 50 and 75% of a seed population. (B) Relationship between GRg and water potential for 25, 50 and 75% of a seed population. Adapted from Batla et al. [74].

Hydrothermal Time (HTT) model: This model extends the basic thermal time model by including both temperature and water potential [67]. It calculates the accumulation of hydrothermal time required for germination fraction (i.e., HTT_{25}, HTT_{50}, HTT_{75}) to occur and is widely used to simulate germination under water stress conditions. This approach was used to study the germination and emergence of *Amaranthus retroflexus* in response to water and temperature stress [75]. The hydrothermal time model has been used to assess the combined effects of temperature and water potential on the germination of *A. retroflexus*, a problematic weed in agriculture. The authors modeled the hydrothermal time required for germination under various environmental conditions, demonstrating that water stress alters the optimal temperature for germination. The HTT model provided a robust framework for predicting weed emergence in varying field environmental conditions, contributing to improved timing of weed control measures.

7. Models to Predict Seed Dormancy and Germination

7.1. Stratification Thermal-Time and Dormancy Induction Thermal-Time

The germination models (i.e., TT, HT and HTT) explained above work well for non-dormant seeds. However, when a seedbank contains seeds with dormancy, it is essential to establish functional relationships between the environmental factors that regulate variations in the dormancy level and the rate-change at which seeds decrease or increase dormancy. Since temperature and water availability are the main factors that regulate these cyclical changes in dormancy level, we must define parameters that accurately characterize these changes. As mentioned above, the changes in seed dormancy can be characterized through the range of temperatures within which seeds can germinate. This range can be characterized by changes in the limit temperatures that allow germination: T_l and T_h and their deviations (Figure 2). To establish functional relationships between time, temperature and dormancy level, Batlla and Benech-Arnold [43] developed a Stratification thermal-time model (S_{tt}; Figure 4a, b) and Malavert et al. [44], Dormancy induction thermal-time (DI_{tt}; Figure 4c, d) for *Polygonum aviculare.* These models quantify seed dormancy release and induction for seeds stratified at different temperatures through changes in the range of temperatures permissive for germination as a consequence of changes in the mean lower limit temperature of the range ($T_{l(50)}$; see Figure 2). These thermal-time approaches are similar to that usual in other weed species to relate germination or emergence processes as a function of time and temperature. However, in contrast to common thermal-time models in which ºCd are accumulated over a T_b, S_{tt} and DI_{tt} accumulate ºCd below or above a ceiling threshold temperature below which dormancy release or above dormancy induction occurs [74].

These models work simultaneously in the accumulation of ºCd after dispersal (*P. aviculare* disperses with a high level of dormancy in early autumn). Due to lower autumn and winter temperatures, the S_{tt} model accumulates more ºCd units (beginning to operate at soil temperatures below 17ºC), allowing the dormancy release process (Figure 4b). Then, as temperatures rise in early spring, the DI_{tt} model begins to accumulate more ºCd than S_{tt} (operating at soil temperatures above 7.9ºC) (Figure 4d). Once DI_{tt} units surpass the accumulation of S_{tt} units, induction into secondary dormancy predominates [44]. The accumulated ºCd can be used to predict how the thermal range permissive for seed germination changes (i.e., widen and narrow) as a consequence of variations in T_l during dormancy release and induction, in relation to soil temperature. Quantifying temperature effects through a thermal-time approach enables predictions of the dormancy level in a seed population exposed to the variable soil field thermal environment. These models are particularly functional, as they predict when the 'emergence window' will open and close and estimate the proportion of seeds likely to emerge within that window.

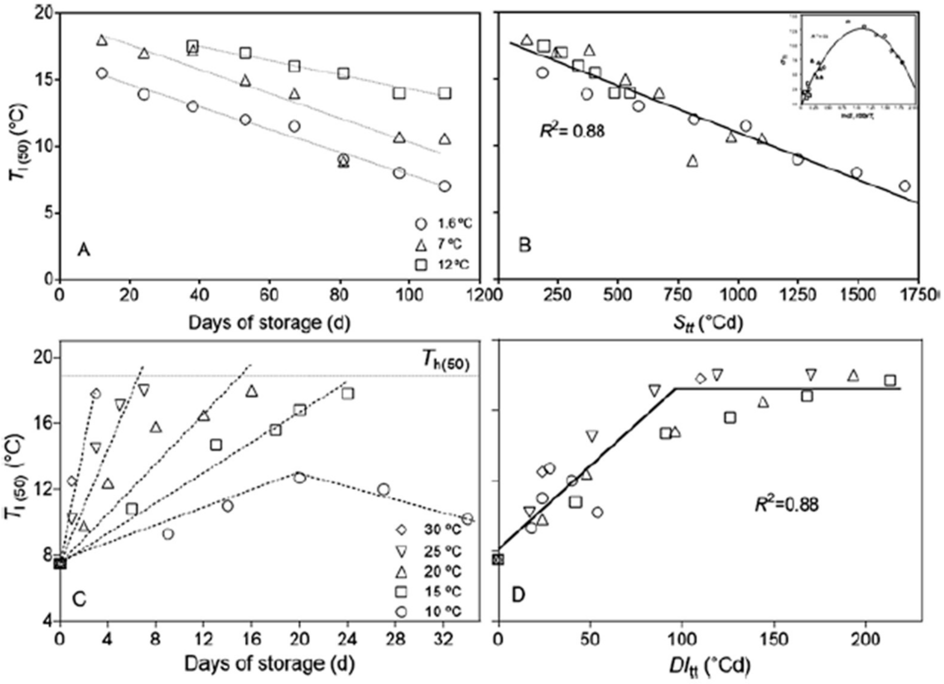

Figure 4. Changes in the mean lower limit temperature ($T_{l(50)}$) for *Polygonum aviculare* seeds during dormancy release and induction. (**a**) Changes in $T_{l(50)}$ during dormancy release for seeds stored at 1.6, 7 and 12°C, plotted

against days of storage and (**b**) against stratification thermal time (S_{tt}). The dotted lines in (**a**) were fitted linear equations for each storage temperature with $R2$ values of 0.98 (1.6°C), 0.84 (7°C) and 0.96 (12°C). The fitted line in (**b**) ($T_{l(50)} = -0.007\ S_{tt} + 18.07$. Inset in (**b**) is estimated values of standard deviation of the lower limit temperature (σ_{Tl}) for *P. aviculare* seeds stored at 1.6, 7 and 12°C plotted against the $\ln(S_{tt}/100)/T_s$, where S_{tt} is the stratification thermal time and T_s is the daily mean storage or soil temperature. The line was fitted according to equation $\sigma_{Tl} = -11.28\ (\ln\ (S_{tt}/100)/T_s)^2 + 23.91\ (\ln\ (S_{tt}/100)/T_s)$ with an R^2 of 0.9. (**c**) Changes in $T_{l(50)}$ during dormancy induction for seeds stored at 10, 15, 20, 25 and 30°C plotted against days of storage and (**d**) against dormancy induction thermal time (DI_{tt}). The dashed lines in (**c**) were fitted by linear equations for each storage temperature with R^2 values of 0.96 (10°C), 0.99 (15°C), 0.87 (20°C), 0.89 (25°C) and 0.96 (30°C), while the dotted straight line indicates the mean higher limit temperature for seed germination of the seed population ($T_{h(50)}$). The fitted bilinear line in (**d**) is the result of repeated regression analysis to obtain the threshold 'dormancy induction temperature' (T_{uDI}) with the best fit according to equation $T_{l(50)} = 0.12\ DI_{tt} + 7.5$, if $DI_{tt} \geq 96.5$°Cd $T_{l(50)} = 18$°C (Figures **a** and **b** adapted from Batlla and Benech-Arnold [43]; figures **c** and **d** adapted from Malavert et al. [44].

Recently, the effect of seed moisture content on the rate of dormancy release and induction in *P. aviculare* seeds was incorporated (Figure 5; [20]). This approach allowed the identification of two seed water content (SWC) thresholds: a minimum value of SWC required to activate metabolic processes in the seeds (the rate at which the process takes place is minimal) and a value which maximizes the velocity of the processes that leads either to dormancy release or to dormancy induction (i.e., 31%) (Figure 5b). The inclusion of the effect of SWC on dormancy changes improved the prediction of seedling emergence in relation to predictions made using only temperature as a driver of dormancy changes [20].

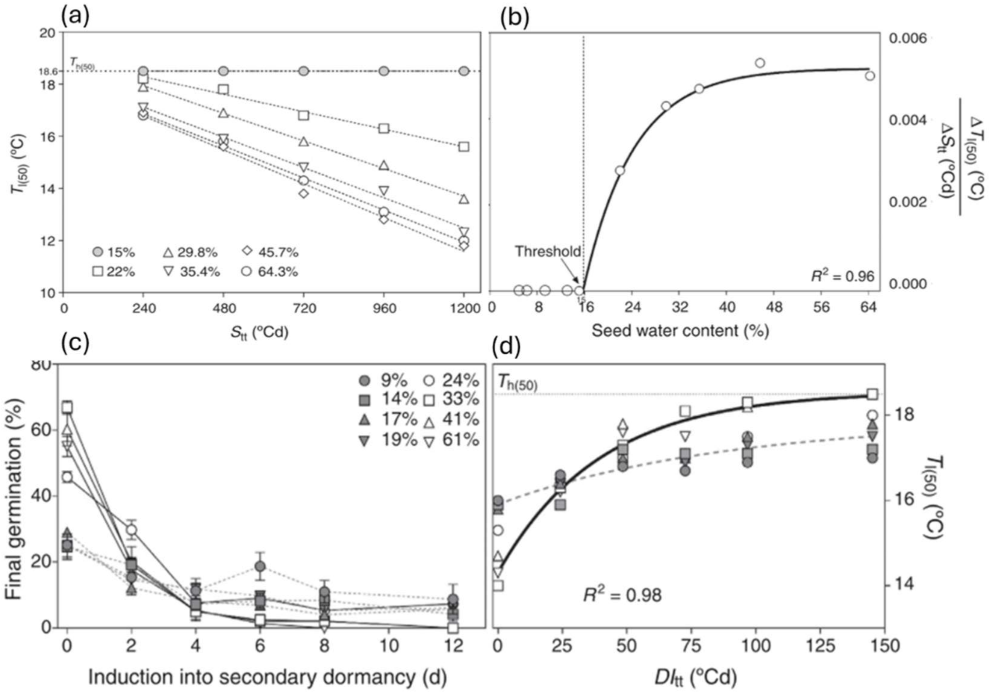

Figure 5. (**a**) Estimated values of the lower-limit temperature for seed germination ($T_{l(50)}$) as estimated from germination curves at 15ºC for *Polygonum aviculare* seeds stratified at 5ºC under different seed water content (SWC) as a function of Stratification thermal-time units (S_{tt}). The dotted-lines were adjusted by linear equations for each SWC with the following R^2 values: 0.98 (22%), 0.99 (29.8%), 0.98 (35.4%) and 0.97 (45.7%) respectively (P-value <0.0001, slope test). (**b**) Dormancy release rate of *P. aviculare* seeds expressed as the decrease in $T_{l(50)}$ per accumulated S_{tt} units during stratification at 5ºC as a function of SWC. The full black line represents the changes in dormancy release rate. The vertical dashed line represents the SWC threshold value (15%) above which the

seeds can perceive the dormancy release effect of low stratification temperatures. (**c**) Final germination for seeds incubated at 15ºC as a function of time during induction into secondary dormancy under different SWC. (**d**) Estimated values of the $T_{l(50)}$ as estimated from germination curves at 15ºC for seeds induced into secondary dormancy at 20ºC under different SWC as a function of dormancy induction thermal-time units (DI_{tt}). The full black line represents the changes in dormancy induction rate, expressed as an increase in $T_{l(50)}$ per accumulated DI_{tt} unit when SWC is above 24%. The dashed line represents the changes in dormancy induction rate, expressed as increase in $T_{l(50)}$ per accumulated DI_{tt} unit when SWC is below 24%. Adapted from Malavert et al. [20].

7.2. After-Ripening Thermal-Time Models

After-ripening (AR) thermal-time models are crucial for understanding the temperature-driven dynamics of seed dormancy release under dry conditions. As explained above, this mechanism is common in winter annuals. More recently, Batlla et al. [76] developed a model for *Arabidopsis thaliana* that associates temperature with dormancy cycling, predicting how seasonal soil temperature fluctuations influence after-ripening and enable germination under favorable conditions. Similarly, Christensen et al. [40] modeled *Bromus tectorum* by simulating dormancy loss during AR process through variations in the base water potential ($\psi_{b(50)}$). In the case of *Lithospermum arvense*, Chantre et al. [41] developed an AR thermal-time model that parameterizes germination taking into account primary dormancy release. Their findings revealed that the rate of dormancy release increases with temperature, making the model a valuable tool for predicting weed emergence. This research demonstrated the potential of AR thermal-time models to support weed management strategies by optimizing predictions of dormancy loss and germination timing based on environmental conditions in autumn-winter species.

The PBTMs offer a promising approach to predicting weed emergence by incorporating the dynamics of seed dormancy and environmental cues. These models use the functional relationships between environmental factors and weed emergence patterns to forecast the timing and extent of seedling emergence. By integrating site-specific environmental data, such as soil temperature and moisture levels, these models can provide precise predictions tailored to specific agricultural landscapes.

8. Application of PBTMs in Site-Specific Weed Management

The PBTMs could be applied in site-specific weed control to predict weed emergence in fields with landscape heterogeneity. This variability most likely leads to weed patches that justify site-specific weed control as a more efficient methodology both from an economic and environmental standpoint. Indeed, factors such as soil temperature and soil water content, previously pointed out as modulators of seed dormancy and germination, can be expected to vary with the position in topography, thus determining variations in weed emergence intensity and temporality. These models could be useful for forecasting the timing and proportion of weeds likely to germinate/emerge differentially based on the part of the topography where they are located, provided we are able to trace the dynamics of soil water content and soil temperature in the various topographic positions. These models consider the changes in seed dormancy as a function of soil temperature and soil water content to accurately forecast the time window for seedling emergence and to provide a notion of the size of the emergence that is taking place within that window. The application of PBTMs in developing georeferenced weed emergence maps enhances precision agriculture by optimizing herbicide use, targeting high-risk areas, and minimizing application in low-risk zones.

For a case study, we selected a location in the agricultural region of Buenos Aires province, in General La Madrid, in the southern part of the province (Lat -37.48; Long -61.41). For the simulation (see ***Simulation model approach*** section in Data supplementary; Table S1), we considered two years with contrasting rainfall patterns (i.e., cold-wet (2017; using daily soil temperature and soil moisture data from the NASA POWER database) and a dry winter (2023), in which water restriction values were hypothetical, designed to represent realistic but conservative conditions for stratification. We assume that *P. aviculare* seeds are homogeneously distributed in the field. Based on this assumption, the model was run from May 1st, when seed dispersion had ended (i.e., around March-April).

To explore how topographic variation influences *P. aviculare* emergence size, simulations were performed across a range of elevation levels (320, 315, 302, 290, 279, and 260 m), using stratification and dormancy induction thermal-time models (S_{tt} and DI_{tt}) and incorporating soil water content (SWC) dynamics. A 20% emergence threshold was used to define the decision point for chemical control, as it represents a balance between effective weed suppression (translated into the economic benefit of yield increase) and the cost of herbicide plus application. This threshold aligns with the concept of economic thresholds in weed science, which define the weed density or emergence level at which the cost of control equals the potential crop yield loss prevented [77–79]. In the absence of *P. aviculare* specific thresholds, this 20% level is supported by empirical studies showing that action thresholds between 15–25% weed emergence or coverage can optimize yield and input efficiency in cereal systems [80,81]. Two contrasting scenarios were simulated: 1) one assuming unrestricted water availability, and 2) another assuming limited soil moisture (see Table S2 and Table S3, Data Supplementary). In the first scenario, the model predicts emergence above the 20% threshold (Figure 6) across all topographic positions from June 17th onwards (Figure S1; Data supplementary).

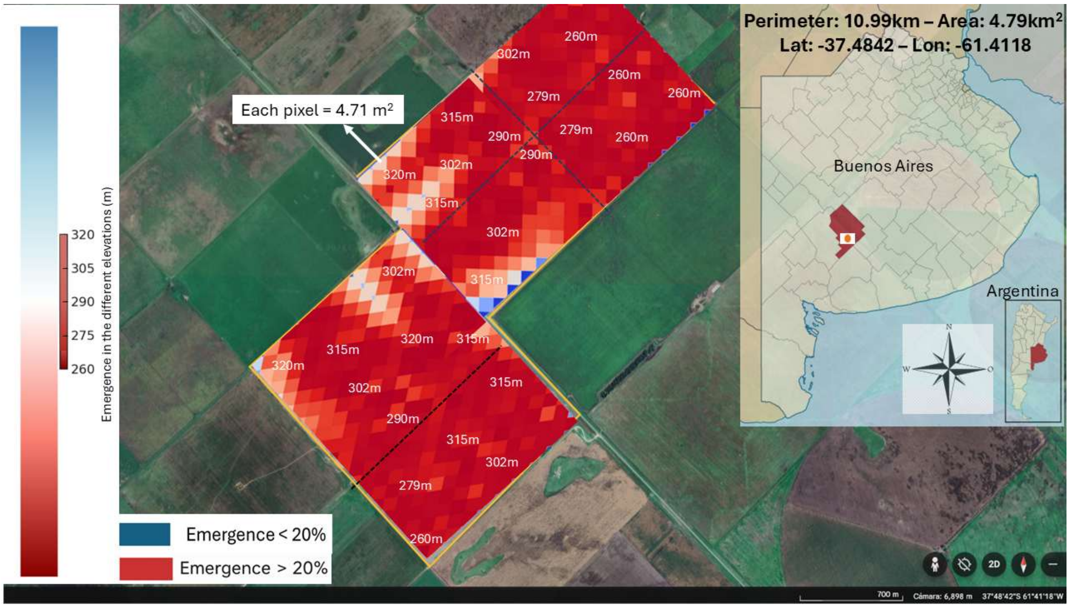

Figure 6. Heatmap showing the simulated emergence proportion of *Polygonum aviculare* at different altitudes in General La Madrid, Buenos Aires Province, under non-limiting soil moisture conditions. In this scenario, emergence exceeded the 20% threshold across all altitudes. The emergence window started on June 17th and closed on September 26th (2017), lasting 103 days. This result reflects optimal stratification and germination conditions. The maps was obtained from Google Earth climate data were retrieved from the NASA POWER database**.**

For the second scenario in the same location, a water restriction during stratification (i.e., cold-dry winter year, 2023) was simulated (see Table S2, Supplementary Data). Under this scenario, SWC was assumed to fluctuate between <15 and 22% throughout the stratification period. These values fall within the range previously identified as the threshold below which dormancy release is either absent or occurs at a minimal rate in *P. aviculare* seeds [20]. This water limitation affected only dormancy dynamics, not germination directly, since the model assumes that germination occurs only after dormancy is lifted and favorable temperature and moisture conditions are met with. In this scenario, the simulation results showed that: i) under cold-dry winter conditions, the model predicts a delay in the onset of emergence, shifting the window to late July (28/07) and early August (08/08) in the lower topographic positions (279 m and 260 m), as opposed to earlier emergence observed in the cold-wet (2017) simulation (i.e., emergence start at 15/06 for 279 and 260 m). Despite this delay, emergence still exceeded the 20% threshold in these lower areas (Figure 7, red pixels). ii) The model predicts that the maximum emergence proportion reaches 24% at 279 m and 42% at 260 m, respectively (Figure S2; Supplementary Data). iii) The emergence window closes approximately 22 days later (August 22nd) and is narrower than in the previous simulation, which extended from June 15th to September 26th, 2017 (103 days in total). This simulation indicates that although at low topographic positions emergence exceeds the 20% indicated as a threshold, under low soil water content, the emergence window becomes more limited in duration, and the overall proportion of seeds able to germinate is reduced as compared with a cold-wet year. In contrast, at higher topographic positions (i.e., 290 to 320 m), the emergence remained below the 20% threshold, precluding chemical control.

This spatial heterogeneity in emergence allows for site-specific herbicide applications, as spraying can be restricted to zones that exceed the control threshold: only the lower topographic positions (260–279 m) would require herbicide treatment in dry years, while higher areas would be spared, potentially reducing herbicide use by up to 60–70%, depending on field topography. This model demonstrates that, even when thermal stratification requirements are met with, if water content is limiting for dormancy release, *P. aviculare* emergence above the 20% threshold would be confined to low topographic positions, where water accumulates and allows dormancy release through S_{tt} accumulation. Although the model focused on soil moisture as the main driver of stratification process, topographic variation could also influence soil temperature and, consequently, emergence patterns. This spatial variation supports the use of georeferenced weed emergence maps and variable-rate sprayers to selectively target areas with higher emergence, reducing chemical use in low-risk zones. Such strategies improve weed control efficiency, reduce costs, and minimize environmental impact.

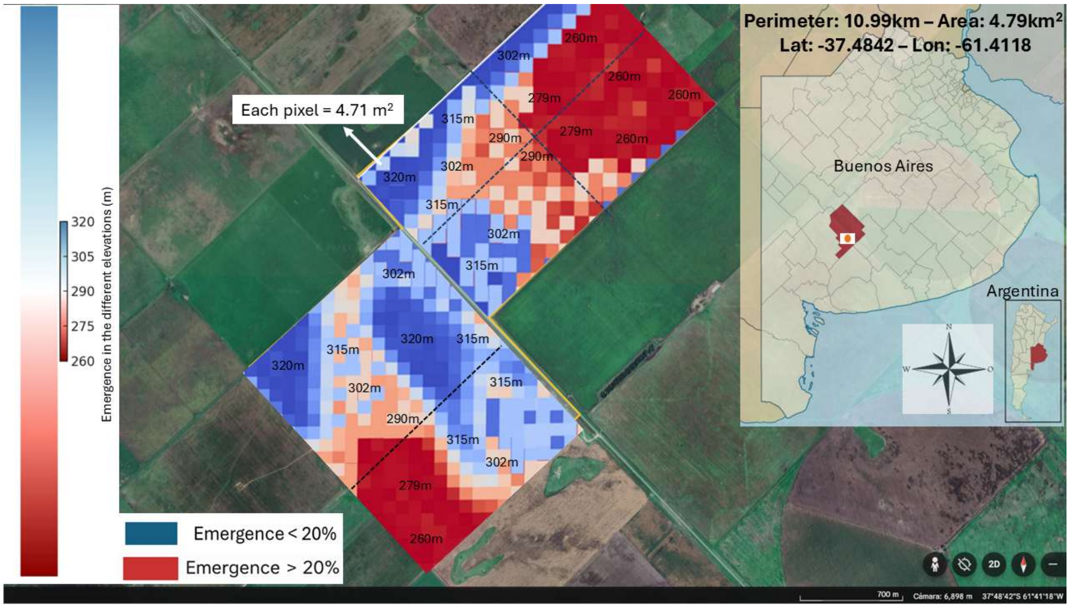

Figure 7. Heatmap showing the simulated emergence proportion of *Polygonum aviculare* at different altitudes in General La Madrid, Buenos Aires Province, under water-limited conditions. Only the lowest altitudes (260 m and 279 m, in red) exceeded the 20% emergence threshold, while higher altitudes remained below it (orange and blue), reflecting spatial variability in soil moisture. The emergence window was delayed (starting between July 28th and August 8th) and shortened, closing on August 22nd (2023). The map was obtained from Google Earth and climate data were retrieved from the NASA POWER database.

In addition to site-specific herbicide applications, weed control in *P. aviculare* can be further optimized through adjustments site-specific in wheat density and sowing date. In wet winters with high predicted weed emergence, increasing wheat sowing density can enhance crop competition, reducing light availability and space for weeds.

9. Conclusions

The problem of troublesome weeds in agricultural fields has increased in recent years [82]. In this regard, the use of Population-Based Threshold Models (PBTMs) in site-specific weed management could represent a significant advancement in agricultural practices, offering a valuable approach for controlling weed emergence with precision and minimum economic and environmental cost [66,83–85]. By integrating dynamic, multidimensional field information, such as soil temperature, soil water content, and topographic variations, and incorporating seedbank dormancy dynamics into these models, PBTMs provide accurate predictions of weed “emergence windows” and proportions [33]. This approach could reduce the risks associated with traditional weed management practices by shifting toward more economically and environmentally sustainable solutions [86], enabling optimized herbicide applications, minimizing input costs, and reducing environmental impact.

Future research should focus on integrating PBTMs with technological advances in agriculture. Precision farming tools, like autonomous machines (self-driving tractors and sprayers), can follow herbicide application maps from PBTMs to target high weed-pressure areas, reducing unnecessary herbicide use. Drones can provide real-time aerial imagery to monitor weeds and assess herbicide effectiveness. Sensors in agricultural machinery can gather data on soil moisture, temperature, and weed emergence, enhancing PBTMs accuracy and enabling precise herbicide application adjustments. Machine Learning (ML) and Artificial Intelligence (AI) can analyze large datasets, improving weed emergence predictions and refining herbicide use. Additionally, Decision Support Systems (DSS) could provide guidance on herbicide applications, incorporating PBTMs outputs and real-time data on weed density, crop health, and weather. Integrating PBTMs with farm management software would allow farmers to manage pest and weed control in one platform (i.e., cellular applications apps), simplifying decision-making and improving overall farm efficiency.

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