



International Journal of Agriculture Development

ISSN (Online): 3107-5347

IJAD 2025; 1(5): 49-53

2025 September - October

www.allagriculturejournal.com

Received: 15-07-2025

Accepted: 20-08-2025

Published: 10-09-2025

DOI: <https://doi.org/10.54660/IJAD.2025.1.5.49-53>

Review on Population Based Threshold Models: A Utility to Measure and Enhance Seed Behaviour

SS Bharath^{*1}, Madhu Chalageri², KC Chandana³

^{1,3} Ph.D. Scholar, Department of Seed Science and Technology, University of Agricultural Sciences, Dharwad, Karnataka, India

² Assistant Professor, Department of Seed Science and Technology, University of Agricultural Sciences, Dharwad, Karnataka, India

Corresponding Author; SS Bharath

Abstract

Seed germination is a complex biological process governed by the inherent diversity within seed populations. Traditional metrics such as germination percentage offer limited insight into the nuanced responses of individual seeds to environmental and physiological factors. Population-based threshold models provide a robust framework for quantifying germination behaviour by incorporating individual seed thresholds distributed normally across a population. These models enable the estimation of key parameters factor-time constant, median base threshold, and standard deviation of thresholds that collectively describe the speed, sensitivity, and variability of germination responses. By fitting germination time-courses to these parameters, researchers can predict responses to hydration, temperature, water potential, plant growth regulators, and storage conditions. This approach not only enhances our understanding of seed dormancy and germination mechanisms but also supports the development of predictive tools for seed performance and viability over time. The review highlights the model's applicability in both natural and agricultural systems and its relevance for seed conservation, quality assurance and crop establishment strategies.

Keyword: Threshold Models, Seed Behaviour, Germination Timing, Hydrothermal Model, Water Potential

Introduction

If seeds fail to germinate and produce viable seedlings, their inherent value remains unrealized, leading to suboptimal productivity. Enhancing efficiency in crop production is therefore crucial—not only to maximize yield but also to minimize agricultural expansion and safeguard natural ecosystems (Folberth *et al.*, 2020) ^[9]. Concurrently, biological strategies for weed control are increasingly targeting the management or eradication of soil weed seed banks. Understanding how seeds perceive and respond to environmental cues is vital for promoting desirable species (such as crops and natives) and suppressing undesirable ones (weeds and invasives) (Long *et al.*, 2015) ^[15]. Modelling seed behaviour, particularly germination responses to environmental factors like temperature (T) and water potential (ψ), both of which are being altered by climate change is essential. These responses are further modulated by the physiological state of the seed, including dormancy

mechanisms that synchronize germination with favourable conditions and seed age or vigour, which determine the seed's functional lifespan.

While seed companies primarily focus on developing new varieties, the ultimate determinant of success lies in seed performance under greenhouse and field conditions, which influences customer retention. Moreover, as the efficacy of certain herbicides declines due to genetic and metabolic resistance in weeds (Perotti *et al.*, 2020) ^[18], managing weed seed production and persistence in the soil seed bank becomes increasingly critical. Quantitative models of seed behaviour especially those accounting for population-level dynamics offer valuable tools for assessing, enhancing and maintaining seed quality. This review introduces new methodologies to facilitate the practical application of such models. Modelling seed behaviour has broad implications for improving stand establishment. Degree-day models, which rely on cardinal temperatures (minimum, optimum and

maximum) for germination, help estimate germination rates and thresholds. A key parameter within these models is germination uniformity across a seed lot. Although standard germination tests are typically conducted under optimal conditions, the variability observed provides an upper bound for field-level uniformity. However, these tests often emphasize total viability and rarely quantify uniformity, leaving a gap in available data.

Understanding seed sensitivity to T and ψ conditions in the seedbed is also critical. Even minor reductions in water availability can significantly impair germination speed and uniformity. In the context of shifting climates, the ability to align seed lots with suitable marketing environments offers a strategic advantage for seed companies. Germination speed, the first trait to decline with seed aging, serves as a key indicator of seed vigour and can be quantified using PBT models. Accurately determining a seed lot's position along the continuum from high vigour to senescence is essential for inventory management and germplasm conservation. Beyond crop performance, effective weed population control remains a cornerstone of sustainable agriculture. Modelling germination and dormancy dynamics within weed seed banks, especially in response to weather patterns, enables the prediction of emergence timing and supports targeted management interventions. This review highlights the importance of understanding and modelling seed germination behaviour especially in response to temperature, water potential and physiological traits for improving crop productivity, managing weed seed banks and adapting seed performance to changing environmental conditions.

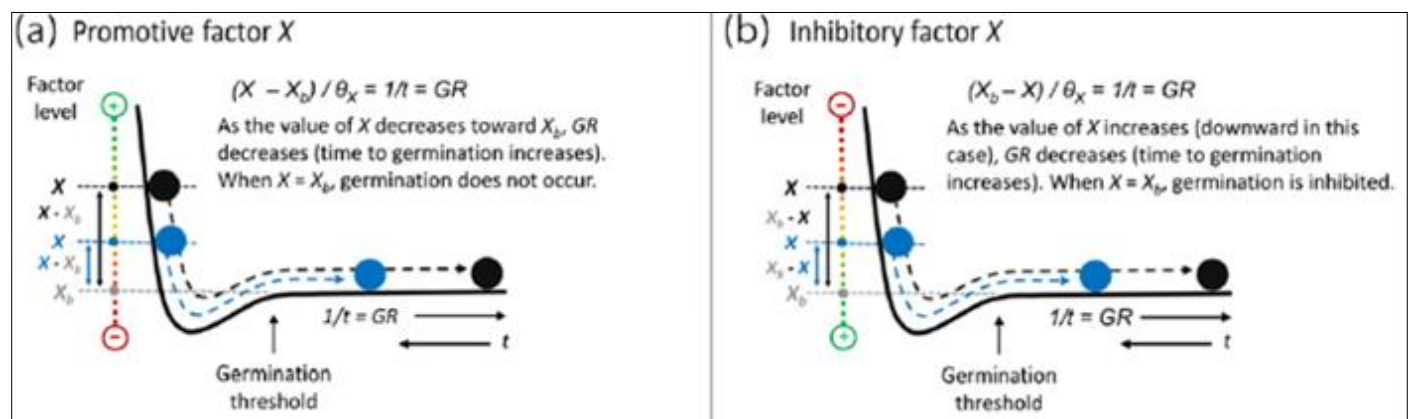
Basis of Population Based Approaches To Seed Biology

Germination marks a decisive and irreversible transition in a seed's life cycle. Once the embryo protrudes from its enclosing tissues, the seed has committed to growth it cannot revert to dormancy. This commitment is a life-or-death decision, hinging on the seed's ability to accurately interpret both internal physiological cues and external environmental signals. If the seed correctly senses favourable conditions, its chances of successful establishment and maturation increase. However, misreading these signals or ignoring negative cues can lead to failure, especially in unpredictable or harsh environments. Over evolutionary time, plants have

developed a wide array of dormancy mechanisms and environmental sensing strategies to navigate this critical decision. These adaptations reflect the immense diversity of plant species and the varied climates they inhabit. While germination is an individual act, the broader success of a species or crop depends on the collective behaviour of seed populations. In both natural ecosystems and agricultural fields, it is the aggregated response of many seeds that determines whether a species thrives or fails (Mitchell *et al.*, 2017)^[16].

Species whose seeds can more reliably predict optimal germination timing tend to persist more successfully in their native environments (Larson and Funk, 2016). Yet, environmental variability introduces uncertainty, prompting seeds to adopt bet-hedging strategies. Within a single population, subgroups may respond differently to the same conditions. Some seeds germinate immediately when temperature and moisture are adequate, potentially gaining a competitive edge through early emergence. However, this strategy carries risk if favourable conditions do not persist, these seedlings may perish. Other seeds remain dormant, bypassing seemingly suitable opportunities and acting as a reserve for future establishment. This diversity in germination timing spreads risk across the population, ensuring that even if many individuals fail, enough succeed to sustain the species over time (Gianella *et al.*, 2021)^[11].

In studying seed behaviour, whether for ecological research or agricultural application it is essential to recognize the dual importance of individual variability and population-level dynamics. The range of germination responses observed within a seed lot is not noise or error, but a reflection of inherent biological diversity. The most common metric used to assess seed performance is germination percentage, which inherently acknowledges that not all seeds behave identically. Any percentage-based measure implies variation among individuals some germinate, others do not; some are dormant, others active; some viable, others dead. This quantal nature of seed responses expressed in binary outcomes like germinated vs. ungerminated or dormant vs. nondormant underscores the complexity of seed biology. Appreciating this diversity is crucial for developing accurate models, improving seed quality assessments, and designing effective management strategies for both crops and weeds.



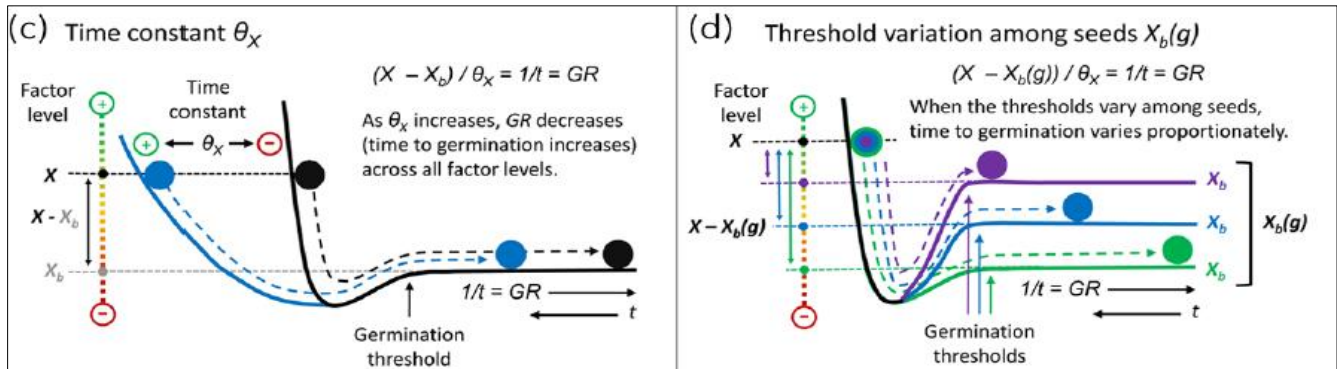


Fig 1 explanation: To conceptually illustrate the features and parameters of population-based threshold (PBT) models, consider the case of a ball rolling down an incline and then rolling up over a subsequent hill (threshold). The distance that the ball would roll on the flat after surmounting the hill represents the germination rate (GR, or $1/t$). (a) In the case of a factor promoting germination (e.g. temperature or GA), decreasing the factor level would lower the starting height of the blue ball, giving it less momentum to overcome the hill (threshold), and it would subsequently roll a shorter distance, indicating a slower GR, or longer time to germination; increasing the factor level would have the opposite effect, speeding germination. If the promotive factor level is reduced to equal X_b , germination is prevented as the ball will not have sufficient momentum to overcome the threshold. (b) To illustrate the effect of germination inhibitors (e.g. more negative ψ or ABA), we reverse the scale on the factor level; that is, lower factor levels increase the height of the ball and GR is increased. As the inhibitory factor level increases (downward on the scale;) it approaches X_b , reducing GR and preventing germination when $X = X_b$. (c) The time constant (θ_x) has the effect of speeding or slowing germination at all factor levels; a shallower slope of the incline illustrates the effect of increasing θ_x . It does not affect the final momentum, so the ball can still overcome the threshold (second hill), but it will delay germination proportionately across factor levels. In the case of suboptimal temperatures, the value of θ_T varies among seeds in the population. (d) For most factors, it is the threshold that varies among seeds, illustrated as variation in the height of the second hill that the ball must climb. Thus, for a given factor level X (starting height on the first hill), the ball will use increasing amounts of momentum to scale the second hill, leaving it with less to proceed on the flat or reducing GR. When the value of X_b increases to equal X , germination is prevented, i.e., the ball would not have sufficient momentum to climb the second hill.

Population Based Models for Environmental Factors Affecting Seed Germination

Seed germination is governed by a series of environmental thresholds, with temperature being one of the most fundamental factors. Population-based models describing germination time courses often rely on the threshold concept, as outlined by Bradford (1995) [3]. A threshold, in this context, refers to the minimum intensity of an environmental input such as temperature that must be exceeded for germination to initiate. For seeds, this translates into a base temperature (T_b), below which germination either does not occur or proceeds infinitely slowly. Once the ambient temperature surpasses T_b , germination becomes possible and its rate increases linearly with temperature. This relationship forms the basis of the thermal time model, which quantifies

the thermal time (θ_T) required for a specific fraction (g) of a seed population to germinate using the equation:

$$\theta_T(g) = (T - T_b) \times t_g.$$

Here, T is the ambient temperature, and t_g is the time required for fraction g to germinate. Because temperature fluctuates diurnally, daily mean temperature is commonly used in thermal time calculations. However, this simplification may not be suitable for all species, as some seeds require alternating temperatures to trigger germination. The concept of thermal time has broad applicability across biological systems, including crop development, pest emergence and other temperature-dependent processes in plants, insects and poikilothermic animals (Trudgill *et al.*, 2005) [22].

In addition to temperature, water availability is another critical factor influencing germination. Seeds require a water potential (ψ) above a certain threshold to initiate germination. Pure water has the highest ψ value (0 MPa) and as ψ becomes more negative, germination is progressively delayed. At the base water potential (ψ_b), germination ceases entirely. Gummerson (1986) [12] introduced a key insight that individual seeds within a population may have different ψ_b thresholds. This led to the development of the hydrotime model, which describes germination as:

$$\theta_H = (\psi - \psi_b(g)) \times t_g$$

Combining temperature and water potential into a unified framework, Gummerson also proposed the hydrothermal time (HTT) model for suboptimal temperature conditions:

$$\theta_{HT} = (\psi - \psi_b(g)) \times (T - T_b) \times t_g$$

This model integrates the dual influence of temperature and water availability, offering a more comprehensive prediction of germination behaviour under variable field conditions. Another environmental factor that significantly affects seed germination is oxygen availability. Oxygen diffusion is much slower in water than in air, which poses challenges for seeds in saturated soils. While some semiaquatic species like rice are adapted to germinate under hypoxic conditions, most seeds experience inhibited germination when oxygen levels fall below 10% (Yentur and Leopold, 1976). Oxygen consumption rates are closely linked to germination rates and are influenced by temperature and water potential in similar ways (Dahal *et al.*, 1996; Bello and Bradford, 2016) [6, 1]. To model oxygen effects, Bradford *et al.* (2007) [7] extended the population-based threshold (PBT) framework to include oxygen, using the following equation:

$$\theta_{Ox} = (\log O_x - \log O_{xb}(g)) \times t_g$$

Here, θ_{Ox} is the oxygen-time constant, O_x is the ambient oxygen percentage, and $O_{xb}(g)$ is the base oxygen threshold

below which germination of fraction g is inhibited. Species-specific Oxb(50) values range widely from less than 1% to over 9% with rice capable of germinating anaerobically at 0.02%. In barley, after-ripening dramatically reduced the oxygen threshold from 36% to 0.3%, enhancing germination in ambient conditions. This change was attributed to increased hull permeability and reduced oxygen sensitivity of the embryo (Bradford *et al.*, 2008)^[5]. Moreover, hypoxia has been shown to amplify the inhibitory effects of abscisic acid (ABA) on dormant seeds (Benech-Arnold *et al.*, 2006)^[2]. Subsequent PBT analyses revealed that oxygen availability modulates hormonal sensitivity, particularly to ABA and gibberellins (GA), further complicating the germination landscape. These findings underscore the intricate interplay between internal physiological states and external environmental cues, especially during dormancy loss and after-ripening.

Other PBT Models for Quantifying Seed Germination Dynamics

The diverse environmental and physiological factors influencing seed germination have led to the development of several Population-Based Threshold (PBT) models, each tailored to quantify specific aspects of seed response. The thermal-time model captures the relationship between temperature and germination rate, using a base temperature (T_b) below which germination does not proceed, and calculating thermal time (θT) as a function of temperature excess and time. Complementing this, the hydro-time model accounts for water availability, defining a base water potential (ψ_b) below which germination is inhibited and modelling germination delay as a function of water stress. These two models are integrated in the hydrothermal time (HTT) model, which simultaneously considers suboptimal temperature and water potential, offering a more comprehensive prediction of germination behaviour under field conditions. Building on this, the hydrothermal priming time model extends HTT principles to quantify the effects of controlled priming treatments on enhancing germination uniformity and speed. The virtual osmotic potential (VOP) model further refines water stress modelling by estimating the effective osmotic potential experienced by seeds, especially under fluctuating moisture conditions. Physiological aging, which affects seed vigour and germination speed, is captured by the ageing time model, linking seed deterioration to delayed or reduced germination performance. Lastly, the oxygen time model addresses the role of oxygen availability, particularly under hypoxic conditions, by defining a base oxygen threshold (Oxb) and modelling germination as a function of oxygen concentration and time. Together, these PBT models provide a robust framework for understanding and predicting seed germination dynamics across diverse environmental scenarios and physiological states.

Summary

Traditional seed vigour tests often expose seeds to stress conditions such as cold, osmotic, or salt stress or accelerate aging through artificial means like controlled deterioration. Others assess seedling growth after a set period. These methods, whether directly or indirectly, influence germination speed or reflect variability in germination timing. Therefore, analysing complete germination time courses offers a more precise and direct approach to evaluating seed vigour. Many seed companies have adopted internal vigour testing protocols that emphasize germination

rate and uniformity, often using smaller sample sizes and testing under suboptimal conditions to identify high-performing seed lots. A critical determinant of seed quality is the physiological maturity at harvest. Ideally, seeds should complete their maturation and dry below the threshold of metabolic activity before collection (Ellis, 2019)^[8]. However, delayed harvesting increases the risk of field weathering, preharvest sprouting and aging all of which degrade seed quality. While postharvest technologies cannot reverse such damage, they can help upgrade seed lots by removing immature or deteriorated seeds.

Seed longevity models have proven valuable for characterizing storage behaviour across species and optimizing conditions for both commercial seed storage and germplasm conservation (Ellis, 1988)^[7]. A persistent challenge in seed bank is the unpredictable loss of viability among seed lots, even within the same species (Fleming *et al.*, 2019; Solberg *et al.*, 2020)^[10, 20]. Periodic viability testing is necessary but consumes seeds from the stored sample. Reducing testing frequency risks falling below the critical viability threshold of 85%, potentially compromising genetic diversity. In this context, Population-Based Threshold (PBT) models offer a promising solution for predicting viability loss and guiding storage decisions.

Seed quality traits such as reduced dormancy can be enhanced through selection and breeding, as seen in domesticated species. However, seed quality often remains a secondary priority for breeders unless it directly affects marketability. For instance, seed shattering continues to hinder production in many crops, especially vegetables (Still and Bradford, 1998)^[21], although recent advances have led to engineered canola varieties with reduced shattering (Lambert *et al.*, 2015)^[13]. Priming techniques are widely used to overcome dormancy and improve uniformity in high-value seeds, offering a practical alternative to breeding out dormancy traits in less-domesticated species. Phenotyping for germination rate (GR) has traditionally been labour-intensive and susceptible to non-genetic variation (Morris *et al.*, 2016)^[17]. Advances in automation are streamlining seed testing and quantitative parameters derived from PBT models are emerging as reliable phenotypic markers for selection (Saux *et al.*, 2020)^[19]. Until seed quality traits are genetically stabilized, models like the hydropriming time model can support the development of efficient seed enhancement protocols. As molecular research continues to unravel the regulatory mechanisms of dormancy and germination, gene editing targets are likely to be identified and applied to improve seed performance.

Despite significant progress in understanding the genetic and physiological foundations of seed vigour and dormancy, further research is needed to elucidate the signalling pathways that translate environmental cues into metabolic and developmental responses. A population-based perspective is essential for designing meaningful experiments. While pooled seed samples may suffice for identifying major genes or mutations, deeper mechanistic insights require single-seed analyses and developmental cohort separation. For example, single-seed assays have revealed dramatic enzyme activity increases up to 1000-fold in germinating seeds, while dormant seeds show no such change. Pooling obscures these differences, leading to misleading interpretations of gradual expression shifts.

Similarly, transcriptomic analyses of pooled imbibed seeds suggest a smooth transition from dormancy-related to germination-related gene expression. However, separating germinated from ungerminated seeds reveals that the former

exclusively express growth-related transcripts, while the latter retain profiles similar to dry seeds. This indicates that ungerminated seeds maintain a dormant physiological state until germination is initiated, at which rapid shift in gene expression occurs. Such seeds must preserve dehydration tolerance mechanisms until commitment, as germination is irreversible.

Adopting a PBT framework fundamentally reshapes experimental design and interpretation in seed biology. It enables researchers to capture the inherent variability and developmental timing within seed populations, offering deeper insights into the causal relationships between environmental signals and biological responses. A population-based approach is not only essential for seed scientists but also instructive for broader biological research.

Conclusion

Population-Based Threshold (PBT) models offer a powerful framework for quantifying seed vigour, dormancy and germination responses under varying environmental conditions. By integrating factors such as temperature, water potential, oxygen availability and aging, these models enable more precise assessment of seed quality and performance. Their application not only enhances seed selection, priming and storage strategies but also supports the development of efficient testing protocols and genetic improvement. As research advances toward molecular and single-seed resolution, adopting a PBT perspective is essential for uncovering the dynamic and diverse mechanisms that govern seed behaviour and for designing biologically meaningful experiments.

References

1. Bello P, Bradford KJ. Single-seed oxygen consumption measurements and population-based threshold models link respiration and germination rates under diverse conditions. *Seed Sci Res.* 2016;26(3):199–221.
2. Benech-Arnold RL, Gualano N, Leymarie J, Côme D, Corbineau F. Hypoxia interferes with ABA metabolism and increases ABA sensitivity in embryos of dormant barley grains. *J Exp Bot.* 2006;57(6):1423–30.
3. Bradford KJ. Water relations in seed germination. In: Kigel J, Galili G, editors. *Seed Development and Germination*. New York: Marcel Dekker, Inc.; 1995. p. 351–96.
4. Bradford KJ, Côme D, Corbineau F. Quantifying the oxygen sensitivity of seed germination using a population-based threshold model. *Seed Sci Res.* 2007;17(1):33–43.
5. Bradford KJ, Benech-Arnold RL, Côme D, Corbineau F. Quantifying the sensitivity of barley seed germination to oxygen, abscisic acid and gibberellin using a population-based threshold model. *J Exp Bot.* 2008;59(2):335–47.
6. Dahal P, Kim NS, Bradford KJ. Respiration and germination rates of tomato seeds at suboptimal temperatures and reduced water potentials. *J Exp Bot.* 1996;47(7):941–7.
7. Ellis RH. The viability equation, seed viability nomographs, and practical advice on seed storage. *Seed Sci Technol.* 1988;16:29–50.
8. Ellis RH. Temporal patterns of seed quality development, decline, and timing of maximum quality during seed development and maturation. *Seed Sci Res.* 2019;29(2):135–42.
9. Folberth C, Khabarov N, Balkovič J, Skalský R, Visconti P, Ciais P, *et al.* The global cropland-sparing potential of high-yield farming. *Nat Sustain.* 2020;3(4):281–9.
10. Fleming MB, Hill LM, Walters C. The kinetics of ageing in dry-stored seeds: a comparison of viability loss and RNA degradation in unique legacy seed collections. *Ann Bot.* 2019;123(7):1133–46.
11. Gianella M, Bradford KJ, Guzzon F. Ecological, (epi)genetic and physiological aspects of bet-hedging in angiosperms. *Plant Reprod.* 2021;34(1):21–36.
12. Gummerson RJ. The effect of constant temperatures and osmotic potentials on the germination of sugar beet. *J Exp Bot.* 1986;37(6):729–41.
13. Lambert B, Denolf P, Engelen S, Golds T, Haesendonckx B, Ruiter R, *et al.* Omics-directed reverse genetics enables the creation of new productivity traits for the vegetable oil crop canola. *Procedia Environ Sci.* 2015;29:77–8.
14. Larson JE, Funk JL. Regeneration: an overlooked aspect of trait-based plant community assembly models. *J Ecol.* 2016;104(5):1284–98.
15. Long RL, Gorecki MJ, Renton M, Scott JK, Colville L, Goggin DE, *et al.* The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. *Biol Rev Camb Philos Soc.* 2015;90(1):31–59.
16. Mitchell J, Johnston IG, Bassel GW. Variability in seeds: biological, ecological, and agricultural implications. *J Exp Bot.* 2017;68(4):809–17.
17. Morris K, Barker GC, Walley PG, Lynn JR, Finch-Savage WE. Trait to gene analysis reveals that allelic variation in three genes determines seed vigour. *New Phytol.* 2016;212(4):964–76.
18. Perotti VE, Larran AS, Palmieri VE, Martinatto AK, Permingeat HR. Herbicide resistant weeds: a call to integrate conventional agricultural practices, molecular biology knowledge and new technologies. *Plant Sci.* 2020;290:110255.
19. Saux M, Bleyss B, André T, Bailly C, El-Maarouf-Bouteau H. A correlative study of sunflower seed vigor components as related to genetic background. *Plants (Basel).* 2020;9(3):386.
20. Solberg SO, Yndgaard F, Andreassen C, von Bothmer R, Loskutov IG, Asdal Å. Long-term storage and longevity of orthodox seeds: a systematic review. *Front Plant Sci.* 2020;11:1007.
21. Still DW, Bradford KJ. Using hydrotimes and ABA-time models to quantify seed quality of Brassica during development. *J Am Soc Hortic Sci.* 1998;123(4):692–9.
22. Trudgill DL, Honek A, Li D, Van Straalen NM. Thermal time – concepts and utility. *Ann Appl Biol.* 2005;146:1–14.
23. Yentur S, Leopold AC. Respiratory transition during seed germination. *Plant Physiol.* 1976;57(2):274–6.

How to Cite This Article

Bharath SS, Chalageri M, Chandana KC. Review on Population Based Threshold Models: A Utility to Measure and Enhance Seed Behaviour. *International Journal of Agriculture Development.* 2025; 1(5): 49-53.

Creative Commons (CC) License

This is an open access journal, and articles are distributed under the terms of the Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International (CC BY-NC-SA 4.0) License, which allows others to remix, tweak, and build upon the work non-commercially, as long as appropriate credit is given and the new creations are licensed under the identical terms.