



EFFECTS OF ENTOMOPATHOGENIC FUNGAL BIO-PRIMING ON GERMINATION PERFORMANCE OF SHALLOT SEEDS UNDER DROUGHT AND SALINITY STRESS

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ABSTRACT

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This study examined how fungal bio-priming with *Beauveria bassiana* and *Metarhizium anisopliae* affected shallot (*Allium cepa* L. var. *aggregatum*) seed germination under drought and salinity stress. This experiment used a factorial experiment with three bio-priming treatments (control, *B. bassiana*, and *M. anisopliae*) and three stress conditions (non-stress, 100 mM NaCl, and drought stress with polyethylene glycol at -0.5 MPa). The results showed that bio-priming and stress conditions together influenced all germination parameters. *B. bassiana* improved germination speed, uniformity, and synchrony under non-stress conditions. Under drought stress, however, hydro-priming (control) achieved the fastest germination timing, while *B. bassiana* still improved germination uniformity relative to the control. *M. anisopliae* showed numerically higher germination speed and velocity under salinity stress, although these differences were not statistically significant among treatments, and this treatment also exhibited greater (though non-significant) variability in germination timing. Drought and salinity both increased germination variability and uncertainty, but fungal bio-priming reduced these effects depending on the stress type. Fungal bio-priming affected not only germination capacity but also the timing and predictability of germination. These findings support using fungal bio-priming to improve shallot seed germination under drought and salinity stress.

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INTRODUCTION

Shallot (*Allium cepa* L. var. *aggregatum*) is important in Indonesia, both as a staple in daily cooking and as a valuable crop for farmers. The quality of planting material and early seedling growth, specifically rapid radicle emergence, robust root establishment, and early shoot development, are key factors in sustainable shallot production. This robust initial developmental phase helps the roots develop, improves how well plants adapt, and supports better water and nutrient uptake later on. Seeds with high vigor emerge quickly and evenly, which leads to a uniform plant population and better resource use. Furthermore, uniform emergence reduces competition among plants because the seedlings develop at a synchronized rate, preventing larger, early-

emerging individuals from disproportionately monopolizing light and soil nutrients at the expense of late-emerging ones (Egli & Rucker, 2012; Vaz Mondo *et al.*, 2013; Mielezrski & Filho, 2012). High-vigor seeds also help maintain steady vegetative growth and improve the chances of good yields in the field (Abati *et al.*, 2018). Focusing on seed quality is an important way to build a resilient shallot production system.

Seed vigor also helps plants handle abiotic stresses like drought, salinity, and extreme temperatures. Seeds with high vigor have stronger physiological traits, which allow them to cope with tough conditions and keep growing steadily under stress (Reed *et al.*, 2022; Hussain *et al.*, 2021; Forni & Borromeo, 2023). In shallots and other *Allium* species, salinity stress often slows the growth of leaves, roots, and bulbs. This happens mainly because of lower transpiration, changes in osmotic potential, and less chlorophyll, which together limit photosynthesis and reduce biomass (Solouki *et al.*, 2023). These issues are especially important during germination and early seedling growth, when plants are most sensitive to osmotic stress.

Water deficit during the initial stages of germination significantly restricts seed imbibition and impairs the enzymatic mobilization of starch reserves. In experimental settings, this drought stress is frequently simulated using polyethylene glycol (PEG). PEG is a high-molecular-weight, non-ionic, and non-plasmolyzing compound with strong water absorption properties; it effectively dehydrates plant tissues to mimic the osmotic constraints of natural field drought (Murillo-Amador *et al.*, 2002). Consequently, this PEG-induced drought stress lowers metabolic activity and delays radicle protrusion, ultimately compromising early seedling establishment (Alshamaileh *et al.*, 2025; Wang *et al.*, 2023). As shallot cultivation expanded into areas with high salinity and water scarcity, finding effective and sustainable ways to reduce the negative effects of osmotic and salinity stress during germination remained a major challenge.

Recent advances in seed technology introduced several methods to improve stress tolerance and support early seedling growth. Seed priming helped start controlled metabolic processes before radicle emergence, which led to more uniform and vigorous germination. More recently, bio-priming combined traditional priming with beneficial microorganisms. This approach activated seeds both physiologically and biologically, encouraged early plant-microbe interactions, and improved germination and stress responses (Farooq *et al.*, 2021).

Recent studies have found that fungal bio-priming with beneficial fungi such as *Trichoderma* spp. and arbuscular mycorrhizal fungi (AMF) can improve seed germination and seedling vigor under abiotic stress (Cardarelli *et al.*, 2022; Sun *et al.*, 2025). Previous studies suggest that these benefits may be linked to higher enzymatic activity, including hydrolytic enzymes that help mobilize reserves and antioxidant enzymes that protect cells from oxidative damage during germination (Al Hijab *et al.*, 2024). Although enzymatic activity was not directly measured in this study, the observed improvements in germination speed and uniformity under stress align with these documented physiological mechanisms.

Most studies on fungal bio-priming have looked at vegetative growth or how plants perform after emerging, but fewer have focused on seed germination, especially under drought or salinity stress. Researchers have also rarely used detailed

germination indices that measure not just final germination, but also how quickly and evenly seeds germinate. As a result, it remains unclear how entomopathogenic fungal bio-priming affects the timing and quality of seed germination under abiotic stress.

This study examined how bio-priming with *Beauveria bassiana* and *Metarhizium anisopliae* affects shallot seed germination under osmotic and salinity stress. Researchers measured germination using several indicators, such as final germination percentage, speed, mean time, rate, variability, synchrony, and uncertainty. They expected that fungal bio-priming would help seeds get ready and cope better with stress, leading to quicker and more even germination. The study focused only on how seeds germinated and did not examine growth after germination. The findings showed that entomopathogenic fungi can affect how seeds respond to stress early on in laboratory settings.

MATERIAL AND METHODS

Plant Material and Experimental Site

Seeds of the shallot cultivar Merdeka F1 were obtained from a certified supplier to ensure genetic purity, uniformity, and high viability. Merdeka F1 is widely grown because of its reliable growth and commercial value. Before the experiment, seeds were checked for uniform size and any physical damage. The study took place at the Laboratory of Plant Eco-Physiology and Nutrition, Faculty of Agriculture, Hasanuddin University, Makassar, Indonesia, from November to December 2025.

Experimental Design

The experiment used a factorial Completely Randomized Design (CRD) with two experimental factors. The first factor was seed bio-priming treatment, consisting of three levels: no fungal inoculation (hydro-priming control), bio-priming with *Beauveria bassiana*, and bio-priming with *Metarhizium anisopliae*. The second factor was abiotic stress condition, which included three levels: non-stress (control), salinity stress, and osmotic stress.

Salinity stress was induced using sodium chloride (NaCl) at a concentration of 100 mM, while drought stress was simulated using polyethylene glycol (PEG 6000) solution with an osmotic potential of -0.5 MPa. The combination of both factors resulted in nine treatment combinations. Each treatment was replicated five times, and each replication consisted of 50 seeds, resulting in a total of 45 experimental units.

Seed Surface Sterilization and Bio-Priming

Before priming, seeds were surface-sterilized using 2.5% sodium hypochlorite solution for 10 minutes, followed by thorough rinsing with sterile distilled water to remove residual disinfectant. Seed bio-priming was performed by soaking the sterilized seeds in fungal suspensions for 20 hours with continuous aeration using an aerator. This 20-hour duration was selected based on previous priming protocols for shallot to ensure optimal seed imbibition and allow sufficient time for fungal propagule attachment to the seed coat without inducing premature radicle emergence. The seed-to-solution ratio was maintained at 1:5 (w/v) to ensure uniform hydration and exposure to fungal propagules (Katriani *et al.*, 2023; Zaiful *et al.*, 2025).

The spore density of *Beauveria bassiana* and *Metarhizium anisopliae* suspensions was adjusted to 10^8 spores mL⁻¹. Control seeds were subjected to hydro-priming using sterile distilled water under identical soaking and aeration conditions.

After priming, seeds were air-dried at room temperature briefly (approximately 1-2 hours) only until surface moisture was removed and seeds did not clump together. This mild drying step facilitates seed handling and prevents decay, while maintaining spore viability on the seed surface for subsequent colonization during germination.

Germination Assay and Stress Application

The germination media were initially moistened with 3 mL of the designated treatment solutions: sterile distilled water for control, 100 mM NaCl solution for salinity stress, or PEG 6000 solution for osmotic stress. The concentration of PEG 6000 required to achieve an osmotic potential of -0.5 MPa was determined using the equation described by Michel and Kaufmann (1973).

Petri dishes were randomly arranged and incubated in a growth chamber maintained at 25 °C, 60% relative humidity, and a 12-hour light/12-hour dark photoperiod. To ensure consistent stress conditions and prevent alterations in concentration or osmotic potential due to evaporation, seeds were carefully transferred to new Petri dishes containing fresh filter paper moistened with 3 mL of the respective solutions every four days during the observation period. Seed germination was assessed daily, with germination defined as the emergence of a visible radicle.

Data Collection and Statistical Analysis

Germination performance was evaluated exclusively using germination-related indices. The observed parameters included final germination percentage (%), germination speed index, mean germination time (d), mean germination rate, variance of germination time, coefficient of variation of germination time, germination synchrony, uncertainty, and germination speed coefficient. All germination traits were calculated based on the number of seeds that successfully germinated, defined as radicle emergence greater than 2 mm, which was recorded daily throughout a 14-day observation period. Germination indices were computed using the SeedCalc package in RStudio (version 2024.12.1) following standard procedures described by Silva *et al.* (2019).

All germination data were subjected to analysis of variance (ANOVA) appropriate for a factorial Completely Randomized Design (CRD). Hypothesis testing was conducted to evaluate the null hypothesis that there were no significant differences among the main effects of fungal bio-priming treatments, abiotic stress conditions, and their interactions, evaluated at a 5% significance level ($p < 0.05$). When the ANOVA indicated significant differences among treatments, mean separation was performed using Duncan's Multiple Range Test (DMRT) at a 5% significance level.

RESULTS

Analysis of variance revealed that all observed germination parameters were significantly affected by the interaction between fungal bio-priming treatments and abiotic stress conditions ($p < 0.05$), indicating that the effects of bio-priming on shallot seed germination were highly dependent on the type of stress imposed. Therefore, results are presented and interpreted exclusively based on interaction effects, as summarized in Figures 1-4 and the corresponding tables.

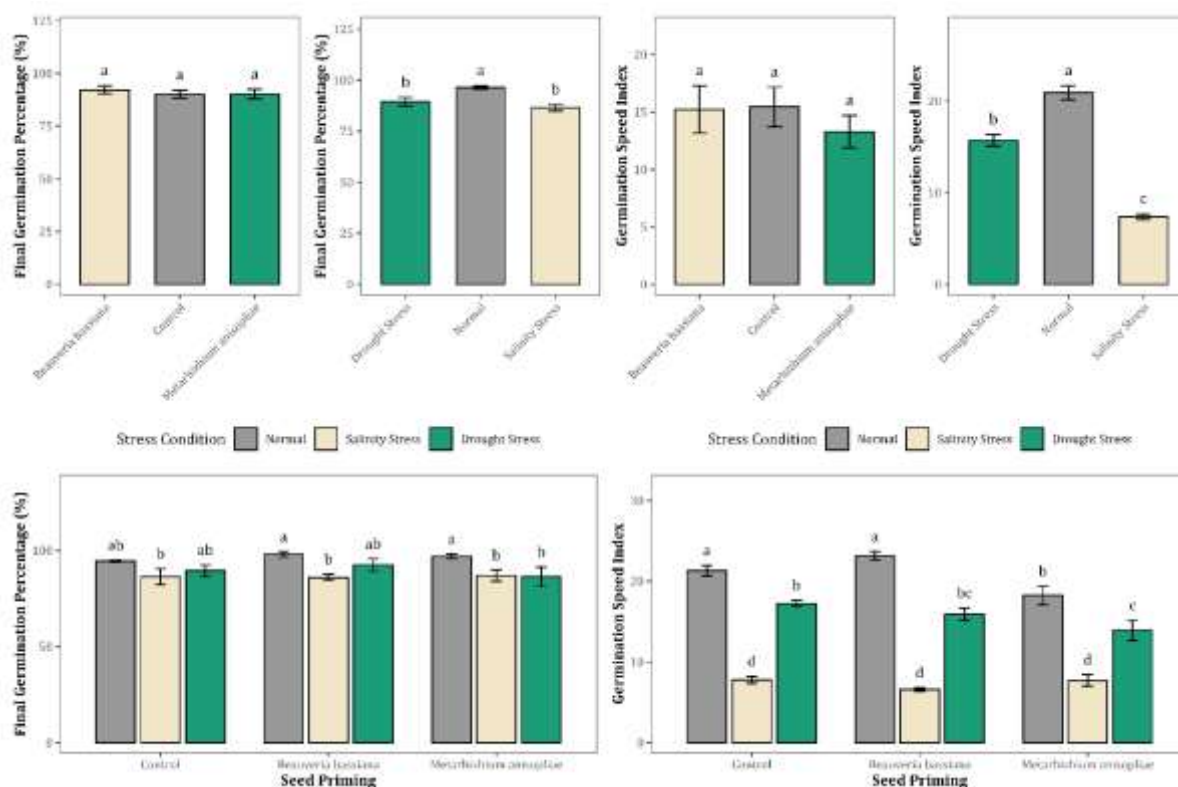


Figure 1. Final germination percentage and germination speed index of shallot (*Allium cepa* L. var. *aggregatum*) seeds subjected to fungal bio-priming (control, *Beauveria bassiana*, and *Metarhizium anisopliae*) under non-stress, drought, and salinity stress conditions. Bars represent means $\pm$ SE. Different letters indicate significant differences (Duncan's test, $p \leq 0.05$).

For final germination percentage (FGP) and germination speed index (GSI) (Figure 1), a significant bio-priming $\times$ stress interaction was detected ($p < 0.05$). Under non-stress conditions, seeds bio-primed with *Beauveria bassiana* exhibited the highest FGP (98.0%), which differed significantly from the control (94.5%) but was statistically comparable to *Metarhizium anisopliae* (97.0%). This pattern was reflected in GSI values, where *B. bassiana* achieved the highest germination speed (23.12), significantly exceeding both the control (21.31) and *M. anisopliae* (18.25). Under salinity stress, FGP decreased markedly across treatments; however, *M. anisopliae* maintained a slightly higher FGP (87.0%) than the control (86.5%) and *B. bassiana* (86.0), although these differences were marginal but statistically distinguished by notation. GSI values under salinity stress were uniformly low (< 8) across all treatments, with no statistically significant differences detected among the control (7.78), *B. bassiana* (6.61), and *M. anisopliae* (7.72), indicating that germination speed under ionic stress was largely comparable regardless of bio-priming treatment. Under drought stress, a contrasting interaction pattern was observed, where *B. bassiana* produced the highest FGP (92.5%) and GSI (15.93), both significantly higher than *M. anisopliae* (86.5% FGP; 13.92 GSI), demonstrating stress-specific efficacy of bio-priming.

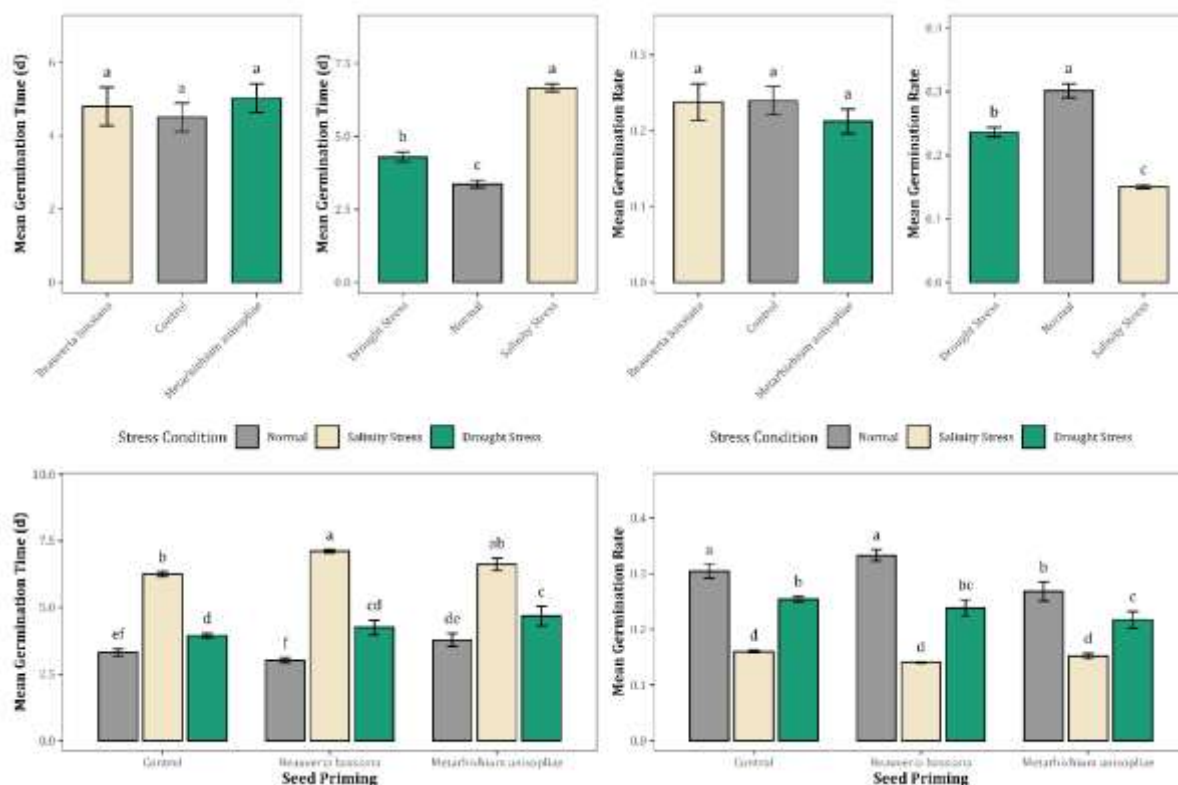


Figure 2. Mean germination time and mean germination rate of shallot seeds following fungal bio-priming under different stress conditions. Bars represent means $\pm$ SE. Different letters indicate significant differences ($p \leq 0.05$).

Mean germination time (MGT) and mean germination rate (MGR) were also significantly influenced by the interaction between bio-priming and stress conditions ($p < 0.05$) (Figure 2). Under non-stress conditions, bio-priming with *B. bassiana* significantly reduced MGT to 3.02 d compared with the control (3.31 d) and *M. anisopliae* (3.78 d), resulting in the highest MGR (0.33). In contrast, under salinity stress, MGT increased substantially for all treatments, with *B. bassiana* exhibiting the longest germination time (7.11 d), which differed significantly from the control (6.25 d) and *M. anisopliae* (6.61 d), as reflected by lower MGR values (0.14). Under drought stress, interaction effects indicated that the control treatment germinated faster (MGT 3.95 d) than fungal bio-primed seeds, while *M. anisopliae* showed the slowest germination (4.68 d) and lowest MGR (0.22), highlighting divergent temporal germination responses depending on stress type.

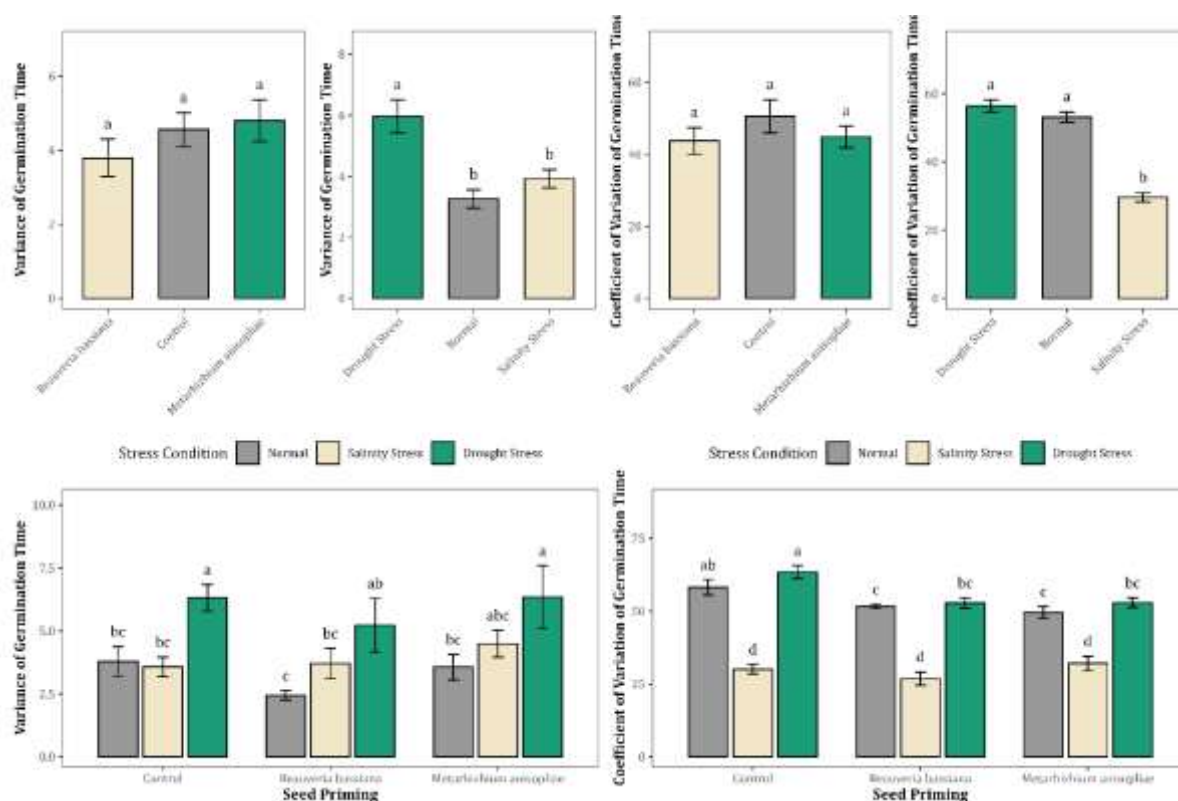


Figure 3. Variance of germination time and coefficient of variation of germination time of shallot seeds under fungal bio-priming and stress conditions. Bars represent means $\pm$ SE. Different letters indicate significant differences ($p \leq 0.05$).

Variance of germination time (VGT) and coefficient of variation of germination time (CVGT) exhibited significant interaction effects ($p < 0.05$) (Figure 3), demonstrating that germination uniformity was jointly regulated by bio-priming and stress conditions. Under non-stress conditions, *B. bassiana* significantly reduced VGT (2.44) and CVGT (51.63) compared with the control (3.79; 58.16) and *M. anisopliae* (3.56; 49.61), indicating more uniform germination, as confirmed by distinct significance letters. Under salinity stress, *M. anisopliae* showed numerically higher VGT (4.49) and CVGT (32.05) than the control and *B. bassiana*; however, these differences were not statistically significant (Duncan's test, $p > 0.05$), indicating that germination timing variability under salinity stress was broadly comparable across bio-priming treatments.

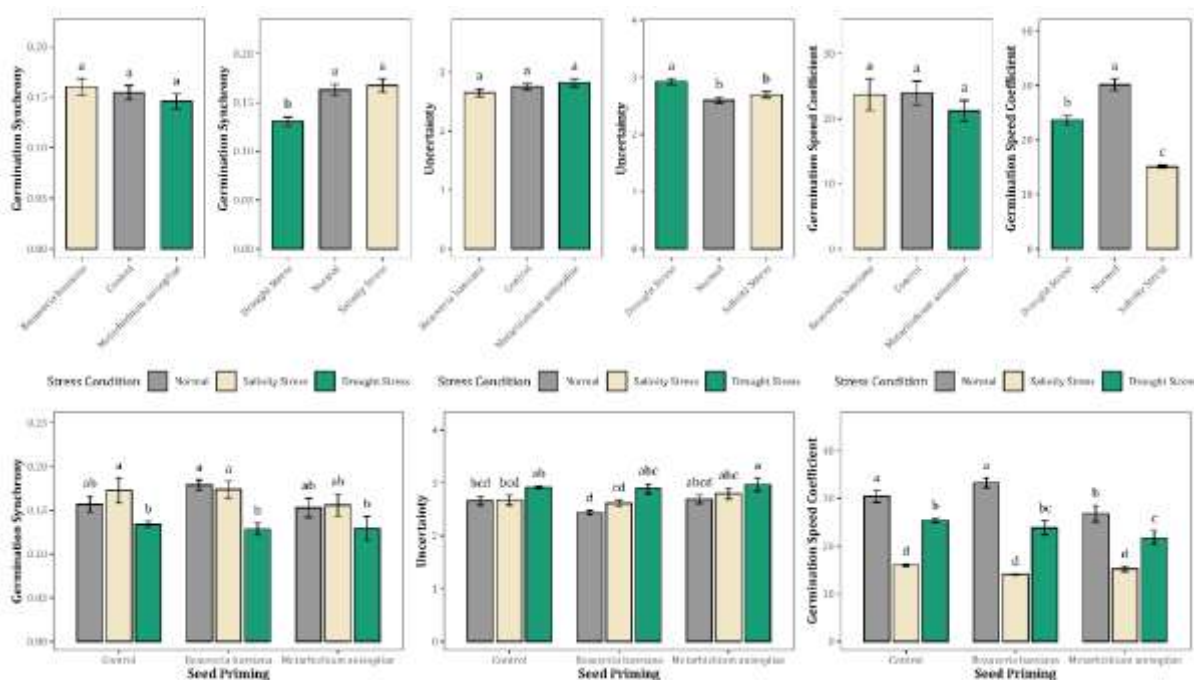


Figure 4. Germination synchrony, uncertainty, and germination speed coefficient of shallot seeds following fungal bio-priming under different stress conditions. Bars represent means $\pm$ SE. Different letters indicate significant differences ($p \leq 0.05$).

Germination synchrony (GS), uncertainty (Unc), and germination speed coefficient (GSC) were likewise significantly affected by the bio-priming $\times$ stress interaction ($p < 0.05$) (Figure 4). Under non-stress conditions, *B. bassiana* produced significantly higher GS (0.18) and GSC (33.26), accompanied by lower uncertainty (2.44 bit), compared with the control (GS 0.16; GSC 30.42; Unc 2.67) and *M. anisopliae* (GS 0.15; GSC 26.79; Unc 2.69), as indicated by differing letter groupings. Under salinity stress, GSC and GS decreased sharply across treatments, with no statistically significant differences among the control, *B. bassiana*, and *M. anisopliae* for GSC. *M. anisopliae* numerically showed the highest uncertainty (2.80 bit), although this value also overlapped statistically with the control and *B. bassiana*. Overall, the consistent significance of interaction terms across all germination indices demonstrates that fungal bio-priming effects on shallot seed germination dynamics are strongly stress-dependent and cannot be interpreted independently of the imposed abiotic conditions.

DISCUSSION

The interaction-driven responses identified in this study can be contextualized within a broader physiological and ecological framework of seed germination under abiotic stress, specifically drought and salinity, as well as the mitigating effects of fungal bio-priming. Although both stressors are well documented to disrupt germination processes, they operate through partially distinct mechanisms, which accounts for the differential interaction patterns observed across various germination indices.

Drought stress primarily constrains germination by limiting water availability, a prerequisite for seed imbibition and the activation of metabolic pathways. Reduced water uptake delays starch mobilization and suppresses enzyme activities essential

for radicle protrusion, resulting in prolonged mean germination time, reduced germination rate, and lower overall germination performance (Ghanifathi *et al.*, 2011; Channaoui *et al.*, 2019; Lateef *et al.*, 2021; Bai *et al.*, 2020; Gheidary *et al.*, 2017). In addition, drought stress has been shown to reduce the activity of α -amylase, thereby restricting the conversion of stored starch into usable energy during early germination (Bai *et al.*, 2020). These physiological constraints explain the interaction patterns in which germination speed, synchrony, and certainty declined markedly under osmotic stress conditions. However, bio-priming has been reported to partially alleviate drought-induced inhibition by enhancing water uptake efficiency and maintaining cellular homeostasis, thereby improving germination dynamics even under limited water availability (Sarkar *et al.*, 2018; Al Hijab *et al.*, 2024).

Salinity stress limits seed germination in two main ways: by causing osmotic stress and ion toxicity. High levels of NaCl lower the water potential outside the seed, making it harder for seeds to absorb water. At the same time, too much Na^+ and Cl^- inside cells disrupts their balance and affects metabolism (Lee & Zhu, 2009; Ibrahim, 2016; Mangena, 2023). Salinity also leads to more oxidative stress, which increases reactive oxygen species and requires stronger antioxidant defenses to protect cells (Yao *et al.*, 2016; Begum *et al.*, 2022). Studies show that high salinity (at or above 100 mM NaCl) greatly lowers the percentage of seeds that germinate, slows down the process, and affects enzymes needed for early seedling growth (Bhat *et al.*, 2025; Ben Youssef *et al.*, 2025). These findings match what was seen in this study, where salinity stress made germination timing more variable and less synchronized.

Bio-priming enables seeds to cope with stress by activating metabolic and protective pathways at the onset of germination. This process induces hydrolytic enzymes such as amylase and lipase, which convert stored reserves into energy and facilitate faster, more uniform germination (Szopińska & Politycka, 2016; Al-Hazmi & Naguib, 2022; Paul & Rakshit, 2023). Additionally, bio-priming enhances the activity of antioxidant enzymes, including superoxide dismutase and catalase, thereby reducing oxidative damage during early germination (Umair *et al.*, 2012; Younesi & Moradi, 2014; Gassoumi *et al.*, 2025). Beneficial microorganisms associated with bio-primed seeds colonize the seed surface and radicle, establishing early symbiotic relationships that promote seedling growth and resilience (Kumar *et al.*, 2025).

Fungal bio-priming has been shown to improve germination under both stress and non-stress conditions. For instance, bio-priming with *Trichoderma harzianum* and *Macrophomina phaseolina* increased germination percentages in canola under optimal conditions (Somagh *et al.*, 2017; Mousavi & Omidi, 2019). *Beauveria bassiana* also enhanced germination rates and seed quality, including shoot and root growth, in maize under non-stress conditions (Kuzhuppillymyal-Prabhakarankutty *et al.*, 2020; Poovarasan *et al.*, 2022). Under salinity stress, *B. bassiana* bio-priming maintained higher germination percentages and improved growth in rice (Akter *et al.*, 2023). These findings are consistent with the interaction effects observed in the present study and indicate that the influence of fungal bio-priming on germination is dependent on the prevailing stress conditions.

M. anisopliae has been shown to improve germination and early growth in several crops. For example, priming wheat seeds with *M. anisopliae* increased germination rates by 13% and 26.04% in different varieties (Bhuiyan *et al.*, 2024). In

maize, it raised germination by 4.34% compared to untreated seeds (Poovarasan *et al.*, 2022). Similar benefits have been seen in barley under drought (Naz *et al.*, 2024) and in rice under salt stress, where treated plants had more biomass and fewer stress markers (Chowdhury *et al.*, 2024). These consistent results across species suggest that the success of fungal bio-priming depends on both the type of microbe and the specific stress the plant faces.

Abiotic stresses affect more than just how many seeds germinate and how quickly they do so. Salinity and drought can delay when seeds start to sprout and spread out the timing, which leads to less synchronized germination (Rashidi & Yadegari, 2014; Singh & Gopal, 2019; El-Katony *et al.*, 2024). Stress also makes germination less predictable, making it harder to know how seeds will perform (Keshtiban *et al.*, 2015; Zare & Moosavi, 2020; Ouahzizi *et al.*, 2023). The results from this study show that bio-priming can help make germination more coordinated and predictable, though the effect depends on how strong and what type of stress is present.

Collectively, these findings reinforce the concept that germination is a dynamic, temporally structured process that is highly sensitive to abiotic stress and microbial intervention. Overall, these results show that germination is a complex process that changes over time and is very sensitive to both stress and microbes. The strong effects seen between bio-priming and stress highlight the need to look at more than just the final germination percentage when studying these responses. By supporting earlier research in different crops and stress situations, this study adds to the evidence that fungal bio-priming can help seeds germinate better in tough conditions, depending on the context.

It is important to note some limitations of the current study. First, the experiment utilized a hydro-primed control to isolate the specific biological effects of the fungal treatments. While this successfully differentiated the microbial impact from the hydration effect, future studies should include a non-primed (raw seed) control to establish a complete baseline of seed performance. Second, although improvements in germination indices suggest positive plant-microbe interactions, this study did not confirm internal tissue colonization through re-isolation assays. Therefore, the observed benefits are attributed to seed surface associations and early symbiotic interactions rather than confirmed endophytic colonization.

CONCLUSION

This study showed that fungal bio-priming influenced shallot seed germination depending on the type of stress. Bio-priming and stress interacted significantly across all germination indices, so fungal treatment effects depended on environmental conditions. Osmotic stress from polyethylene glycol and salinity stress from sodium chloride both reduced germination capacity, speed, uniformity, synchrony, and predictability. Bio-priming with *B. bassiana* performed best under non-stress conditions, increasing final germination percentage, speeding germination, shortening mean germination time, and making germination more synchronized and predictable. Under osmotic stress, however, hydro-priming (control) resulted in faster germination times than fungal treatments. Under salinity stress, germination speed and capacity did not differ significantly among bio-priming treatments, although *M.*

anisopliae showed numerically higher mean values alongside greater (non-significant) variability in germination timing. These results showed that entomopathogenic fungi played different roles during germination depending on the type of stress, highlighting that biological interventions must be carefully matched to specific abiotic challenges.

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Conflicts of interest

The authors declare no known financial or personal conflicts of interest that could have influenced the work reported in this paper.

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