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Effectiveness of Biopriming Using Dark Septate Endophytes in Improving Seed Viability and Early Seedling Growth of *Gmelina arborea* Roxb. ex Sm

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Abstract

Gmelina arborea *is a fast-growing tree species widely cultivated in plantations and community forests, but the low quality of seeds and seedlings often hampers its cultivation. One way to improve the vigor and viability of declining seeds is through priming. This study aimed to assess the effectiveness of dark septate endophyte (DSE) priming treatment in improving seed germination and seedling growth of* G. arborea*. Eight priming treatments (control, soaking seeds in* Cladosporium teunissimum*,* Exophiala pisciphila*,* Cladophialophora nyingchiensis*,* Diaporthe pandanicola*,* Cylindroccarpon *sp., DSE-consortium, and GA3) were set in a completely randomized design. The treatments significantly (p-value ≤ 0.05) affected germination capacity, germination speed, mean germination time, vigor index, shoot (hypocotyl) length, seedling height, diameter, and sturdiness quotient, but not radicle length or germination value. Soaking seeds in C. teunissimum gave the highest germination capacity (87.25%), followed by soaking in E. pisciphila (85.25%) and DSE-consortium (81.25%). Soaking in C. teunissimum resulted in the highest seedling height with an increase in control of 7.6%, while the DSE consortium produced the highest diameter with an increase in control of 10.7%. These findings support the application of DSE-based seed treatments as a promising, sustainable approach to improving seed quality and establishing plantations and community forests.*

Keywords:*biopriming, Gmelina arborea, germination, invigoration, seed and seedling quality*

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Introduction

Gmelina arborea Roxb. is a potentially fast-growing tree species widely cultivated in Indonesia in community forests and industrial plantations (Roshetko et al., 2004; Therapy et al., 2020; Sudrajat & Rustam, 2020). This species grows naturally in South and Southeast Asia, from Pakistan and Sri Lanka to Myanmar, and has been widely introduced to several Southeast Asian countries, such as Thailand, Vietnam, Indonesia, and the Philippines (Jensen, 1995). *G. arborea* thrives in dry deciduous woods and tropical rainforests and is tolerant of a wide range of land conditions at elevations of 0–1,200 m asl with annual rainfall between 750 and 5,000 mm. It grows well at an average temperature of 21–28 °C (Jensen, 1995), in deep, well-drained soils, and at a pH between 5.0 and 8.0 (Hossain, 1999). *G. arborea* wood has strength class III and durability class IV, which is potentially used for light construction, plywood, particleboard, furniture, matches, general carpentry, packaging, fuelwood, and charcoal (Hossain, 1999; Sudrajat & Rustam, 2020). In addition to the wood, the other parts of the *G. arborea* plant, such as the bark, roots, and fruit, contain many pharmacological functions, such as anti-diabetic, anti-oxidant, antiulcer, anti-inflammatory, anti-nociceptive, anticancer, wound healing, and analgesic (Arora & Tamrakar, 2017; Warrier et al., 2021; Priatna et al., 2024; Bhattacharyya et al., 2025; Priatna et al., 2025).

According to Siregar et al. (2020), *G. arborea* can be easily propagated generatively, but the availability of seeds for large-scale seedling production is often hampered by low seed germination. Its seed storage also remains problematic because seeds quickly lose viability in short-term storage (Prakash, 1991; Naithani et al., 2006). Sudrajat et al. (2022) reported that the average germination rate of seeds circulating in the market is less than 70%, while Siregar et al. (2020) argue that the germination rate of *G. arborea* seeds after one year of storage is 72%. *G. arborea* seeds are rated as moderate in terms of drying sensitivity (Naithani et al. 2006). However, these seeds are also close to orthodox characters regarding storage behavior. Generally, these seeds will experience a decrease in germination capacity after 90 days of storage (Naithani et al., 2006).

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One way to improve the vigor and viability of declining seeds is through priming (Syamsuwida et al., 2020; Yuniarti et al., 2023). Priming is a seed treatment designed to accelerate germination, increase seedling uniformity, improve seed and seedling quality, and produce better plants (Shahrajabian et al., 2021; Thakur et al., 2022; Chakraborti et al., 2022). This technique can be implemented in several ways, including physical, chemical, and/or biological methods (Abhilash et al., 2020; Thakur et al., 2022). According to Singh et al. (2023), seed biopriming is a powerful and valuable technology for achieving successful and sustainable ecosystem restoration. However, this technology is rarely applied to Indonesian tropical tree seeds (Yuniarti et al., 2023). One promising technique is biopriming using dark septate endophytes (Surono et al., 2024). Dark septate endophytes (DSE) have the potential to improve seed germination (Widyani et al., 2024; Surono et al., 2024), increase plant growth (Andrade-Linares et al., 2011; Vergara et al., 2018), and increase resistance to biotic and abiotic stresses (pests and diseases) (Surono & Narisawa, 2017; Andriyanto et al., 2024). Biopriming can protect seeds against soil-borne pathogens and promote germination rates and uniformity, increasing primary productivity and soil health (Surono et al., 2024). The application of biopriming in the production of forest tree seedlings will increase productivity and the success of sustainable forest management. This study aims to assess the effectiveness of biopriming treatment using DSE in improving seed germination and seedling growth of *G. arborea*.

Methods

Materials *G. arborea* seeds were collected from the Seed Production Area at the Parungpanjang Research Forest, Bogor, Indonesia, at the coordinates of S6°20′42″ and E106°06′15″. The elevation of the area is 52 m asl with an average annual rainfall of 2,440 mm, with the highest rainfall usually occurring between December and February (Sudrajat et al., 2018; Chaerani et al., 2019). The seeds were processed at the Seed Testing Laboratory, Center for the Implementation of Environmental and Forestry Standards and Instruments (CIEFSI), Bogor, and stored for 1 year at a moisture content of 10.6% in an air-conditioned (AC) room (temperature 18–20 °C, relative humidity 60–70%). Five DSE isolates were obtained from the Applied Microbiology Laboratory, National Research and Innovation Agency, Cibinong, Bogor, i.e., *Cladosporium teunissimum, Exophiala pisciphila, Cladophialophora nyingchiensis, Diaporthe pandanicola*, and *Cylindrocarpon* sp. The isolates were isolated from rice (*Oryza sativa*) roots (*C. teunissimum*), oil palm (*Elaeis guineensis*) roots (*E. pisciphila, C. nyingchiensis,* and *D. pandanicola*), and *Pinus merkusii* roots (*Cylindrocarpon* sp.).

DSE preparation This study used five single strains (*C. teunissimum, E. pisciphila, C. nyingchiensis, D. pandanicola*, and *Cylindrocarpon* sp.) and one DSE consortium. The DSE suspension preparation follows Andrade-Linares (2011), modified by Surono and Narisawa (2017). DSE suspension was formulated by incubating it in 250 ml of potato dextrose broth media at 27 °C and placing it on a rotary shaker at 170 rpm for 14 days. The mycelia were filtered with filter paper and rinsed with distilled water three times or until the liquid became clear. Next, the mycelia were crushed using a blender at a minimum speed for one minute, and distilled water was added. The DSE consortium was created by mixing the five DSE strains above (*C. teunissimum, E. pisciphila, C. nyingchiensis, D. pandanicola,* and *Cylindrocarpon* sp.) in equal proportions. The hyphal density of the DSE solution is in the range of 90 to 177 ml^{-1}.

Experimental design and parameter measurement The DSE prepared for seed treatment is a liquid, which involves seed soaking. *G. arborea* seeds were sterilized by soaking in 5% sodium hypochlorite (NaOCl) for 4 minutes to remove bacterial and fungal contaminants, then rinsed with distilled water (Tuheteru et al., 2022). This biopriming comparison treatment was soaking in GA3, which has been used for priming tropical tree seeds (Siregar et al., 2020; Sudrajat et al., 2022; Yuniarti et al., 2023). The study used a completely randomized design to test eight treatments, i.e., control, soaking seed in *C. teunissimum* solution, soaking seed in *E. pisciphila* solution, soaking seed in *C. nyingchiensis* solution, soaking seed in *D. pandanicola* solution, soaking seed in *Cylindrocarpon* sp. solution, soaking seed in DSE consortium solution, and 250 ppm GA3. Seed soaking in DSE and GA3 solutions was carried out for 24 hours (Surono et al., 2024) with a proportion of 100 seeds soaked in 100 ml of DSE or GA3 solution. Each treatment was repeated 4 times, with the number of seeds per replication being 100 seeds.

Germination tests were conducted in the CIEFSI Bogor greenhouse (relative humidity 69–75%, temperature 29–34 °C). The seeds were sown directly after soaking in the DSE and GA3 solution for 24 hours. Seeds were sown in a germination tray measuring 36 cm 29 cm 15 cm (length width height) containing fine sand that had been sterilized by steaming for 1 hour. Watering was carried out daily while paying attention to the humidity of the sowing medium. Germination observations were done daily by counting the normal seedlings (grown with two pairs of fully developed leaves) (Sudrajat et al., 2017). The germination parameters calculated were germination capacity, germination speed, mean germination time, germination value, radicle length, shoot length, and vigor index, with each formula as shown in Equations *[1]* to *[7]* (Sudrajat et al., 2024; Yuniarti et al., 2025).

$$\text{Germination capacity} = \frac{\text{Number of normal seedling}}{\text{Number of sown seed}} \times 100\% \qquad [1]$$

$$\text{Germination speed} = \frac{N1}{D1} + \frac{N2}{D2} + ... + \frac{Nn}{Dn} \qquad [2]$$

$$\text{Mean germination time} = \frac{(N1T1) + (N2T2) + ... + (N2T2)}{\text{Number of germinated seed}} \qquad [3]$$

$$\text{Germination value} = PV \times MDG \qquad [4]$$

$$PV = \frac{\text{Maximum seed germination percentages on any day}}{\text{Number of days to reach the percentages}} \qquad [5]$$

$$MDG = \frac{\text{Percentage of germinated seed at the end of the test}}{\text{Number of days}} \qquad [6]$$

$$\text{Vigor index} = \text{Germination capacity} \times (\text{shoot length} + \text{radicle lengh}) \qquad [7]$$

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note: *N* = number of seeds that germinate in a certain unit of time (n^{th} day), *D* = n^{th} day of observation, *T* = amount of time between the start and end of the testing interval, *PV* = peak value, and *MDG* = mean daily germination.

Normal seedlings from each treatment at the end of the germination test were transferred to polybags measuring 15 cm 10 cm (in height and diameter), containing a mixture of soil, rice husk charcoal, and compost (3:1:2, by volume). The medium had a pH of 6.0 with a cation exchange capacity of 26.23 $Cmol^{(+)}$ kg^{-1}, a total N content of 0.12%, C-organic 2.125, a ratio of C/N 10, Ca 11.10 $Cmol^{(+)}$ kg^{-1}, Mg 7.08 $Cmol^{(+)}$ kg^{-1}, K 3.53 $Cmol^{(+)}$ kg^{-1}, and P_2O_5 (available) 33.2 ppm. A completely randomized block design was used to test the effect of seed invigoration on the early growth of *G. arborea* seedlings, with four replications, each consisting of 20 seedlings. The seedlings were placed in seedling racks in a nursery with 70% shade. The seedlings were maintained by watering and weeding until they were two months old, after which measurements were taken. The seedling growth parameters measured were seedling height, diameter, and sturdiness quotient (the ratio between seedling height in cm and seedling diameter in mm) (Nurhasybi et al., 2019).

Data analysis Data were analyzed using SPSS version 26.0 (IBM SPSS Statistics). The Shapiro-Wilk normality test showed that most of the data were normally distributed, namely germination capacity (*p*-value = 0.2154), germination speed (*p*-value = 0.3012), mean germination time (*p*-value = 0.4732), and vigor index (*p*-value = 0.991), while for germination value (*p*-value = 0.0078), radicle length (*p*-value = 0.001), and shoot length (*p*-value = 0.0001), the data were not normally distributed so they needed to be transformed. Data transformation for germination value, radicle length, and shoot length used log transformation, inverse transformation, and Box-Cox transformation, respectively (Osborne, 2002). The *p*-values of the normality tests, resulting from the data transformation of germination value, radicle length, and shoot length, were 0.1221, 0.1394, and 0.1495, respectively, indicating that the three data sets were normally distributed.

Analysis of variance was used to test the effect of seed priming using DSE and GA3 on seed viability (germination capacity) and vigor (germination speed, mean germination time, germination value, radicle length, shoot length, and vigor index) of *G. arborea*. Duncan's multiple range test at a 95% confidence level (*p*-value ≤ 0.05) was employed for further testing of germination and vigor parameters that were significantly affected by priming treatments to determine the significant differences between treatments.

Result

The priming treatment using DSE and GA3 significantly affected *G. arborea* seed germination capacity (*p*-value = 0.012), germination speed (*p*-value = 0.018), and shoot (hypocotyl) length (*p*-value = 0.000), but did not significantly affect radicle length (*p*-value = 0.732). The treatment also significantly affected mean germination time (*p*-value = 0.004) and vigor index (*p*-value = 0.001), but did not significantly affect germination value (*p*-value = 0.577). This study found that soaking *G. arborea* seeds in DSE can potentially improve their viability (germination) and vigor.

Soaking seeds in *C. teunissimum* (T-1) resulted in the highest germination capacity (87.25%), followed by *E. pisciphila* (85.25%) and the DSE consortium (81.25%). Soaking seeds in *C. teunissimum* increased the seed germination capacity by 28.3% compared to the control (Figure 1). This treatment also increased germination capacity (44.9%), shoot length (10.9%), mean germination time (13.8%), and vigor index (35.3%) compared to the control. Of the five DSE strains and one consortium, the DSE treatments that consistently had a positive effect on *G. arborea* seed germination compared to the control, especially for the parameters of germination capacity, germination speed, shoot length, mean germination time, and vigor index, were seed soaking in *C. teunissimum* (T-1), *E. pisciphila* (T-2), and the DSE consortium (T-6). Meanwhile, the 250 ppm GA3 treatment could not improve *G. arborea* seed germination and was generally not significantly different from the control (Figure 2 and Table 1).

Priming treatment had a substantial effect on seedling height (*p*-value = 0.000), root collar diameter (*p*-value = 0.000), and sturdiness quotient (*p*-value = 0.000) in *G. arborea*. The treatment of seed soaking in *C. teunissimum* (T-1) produced the highest seedling height (48.60 cm) or an increase of 7.6% compared to the control. In contrast, for root collar diameter, the DSE consortium treatment (T-6) produced the highest diameter of 3.08 mm or an increase of 10.7% from the control. For the sturdiness quotient, seed soaking in *C. teunissimum* gave the highest value (17.10), while the DSE consortium treatment produced the lowest sturdiness quotient value (14.55) (Figure 3 and Table 2). Some DSE, such as *E. pisciphila, C. nyingchiensis*, and *Cylindroccarpon* sp., gave height and diameter growth below

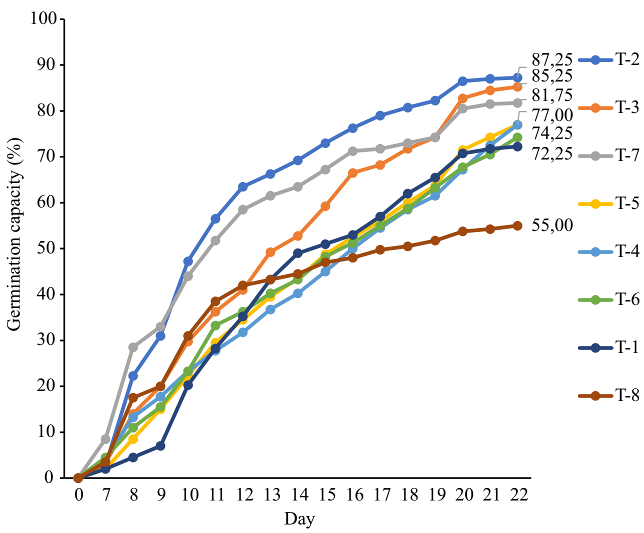

Figure 1 Germination dynamics of *Gmelina arborea* treated by DSE- based biopriming and GA3. Notes: T-0 = control, T-1 = soaking seeds in *C. teunissimum*, T-2 = soaking seeds in *E. pisciphila*, T-3 = soaking seeds in *C. nyingchiensis*, T-4 = soaking seeds in *D. pandanicola*, T-5 = soaking seeds in *Cylindrocarpon* sp., T-6 = soaking seeds in DSE consortium, T-7 = soaking seeds in GA3 250 ppm.

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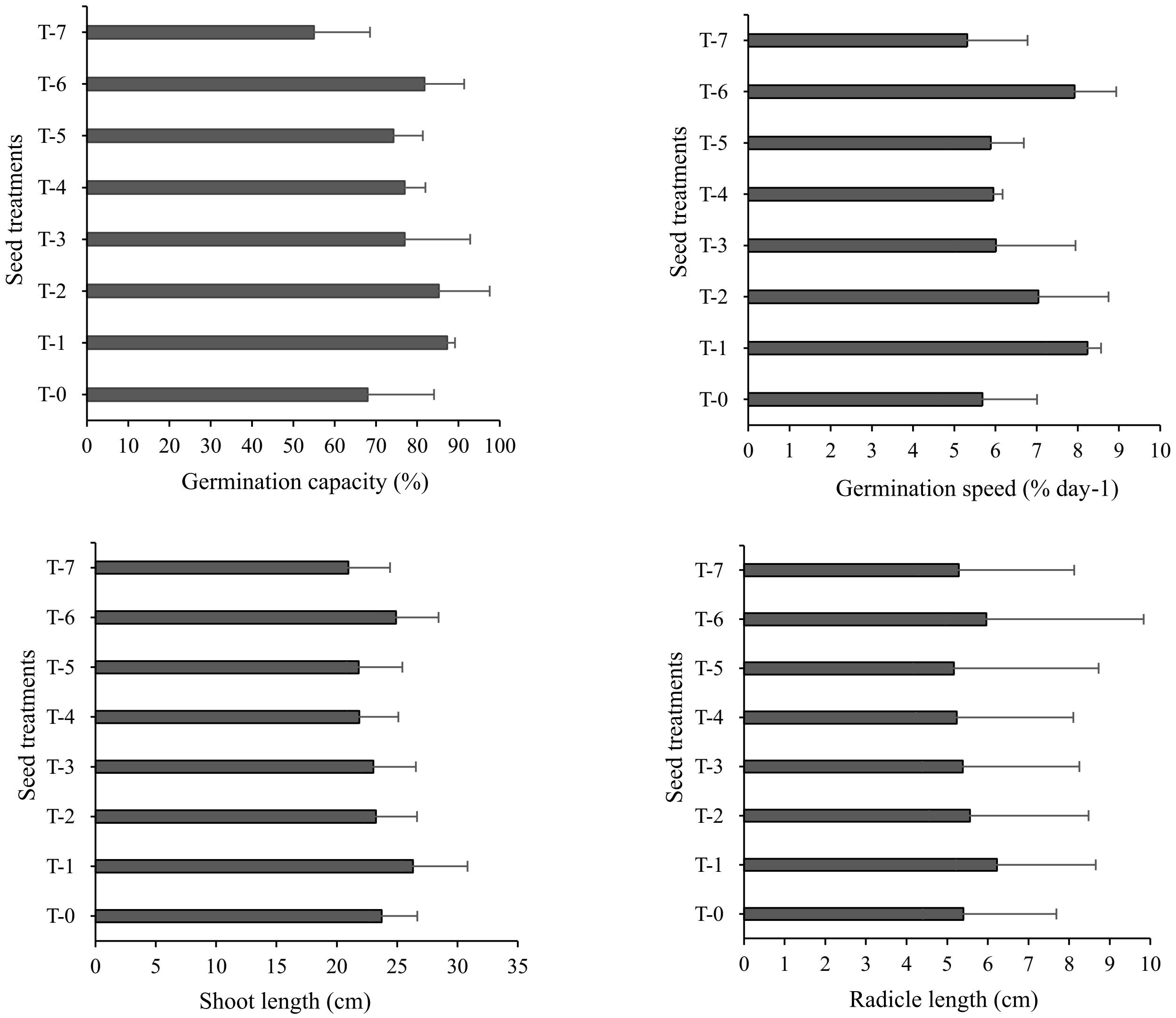

Figure 2 Germination capacity, germination speed, shoot length, and radicle length of *Gmelina arborea* treated by seed priming using DSE and GA_3. Notes: T-0 = control, T-1 = soaking seeds in *C. teunissimum*, T-2 = soaking seeds in *E. pisciphila*, T-3 = soaking seeds in *C. nyingchiensis*, T-4 = soaking seeds in *D. pandanicola*, T-5 = soaking seeds in *Cylindroccarpon* sp., T-6 = soaking seeds in DSE consortium, T-7 = soaking seeds in GA3 250 ppm.

Table 1 Mean germination time, germination value, and vigor index of *Gmelina arborea* treated by DSE-based biopriming and GA3

Seed treatments	Mean germination time (day)	Germination value	Vigor index
T-0	13.25 ± 1.72 a	0.078 ± 0.04	21.01 ± 2.37 b
T-1	11.41 ± 0.47 b	0.286 ± 0.34	28.41 ± 2.74 a
T-2	13.31 ± 1.88 a	0.202 ± 0.18	24.79 ± 5.55 ab
T-3	14.34 ± 1.47 a	0.200 ± 0.20	21.91 ± 4.88 b
T-4	13.90 ± 0.77 a	0.125 ± 0.07	20.97 ± 3.97 b
T-5	13.63 ± 1.03 a	0.198 ± 0.14	20.11 ± 4.15 b
T-6	11.36 ± 0.98 b	0.465 ± 0.53	25.06 ± 0.88 ab
T-7	11.22 ± 0.75 b	0.230 ± 0.10	14.30 ± 3.19 c
p-value	0.004*	0.577^{ns}	0.001**

Notes: The same letters following numbers ($\bar{x}$ ± standard deviation)in the same column indicate no significant difference, * = significant at 95% confident level, ** = significant at 99% confident level, ns = no significant, T-0 = control, T-1 = soaking seeds in *C. teunissimum*, T-2 = soaking seeds in *E. pisciphila*, T-3 = soaking seeds in *C. nyingchiensis*, T-4 = soaking seeds in *D. pandanicola*, T-5 = soaking seeds in *Cylindroccarpon* sp., T-6 = soaking seeds in DSE consortium, T-7 = soaking seeds in GA3 250 ppm.

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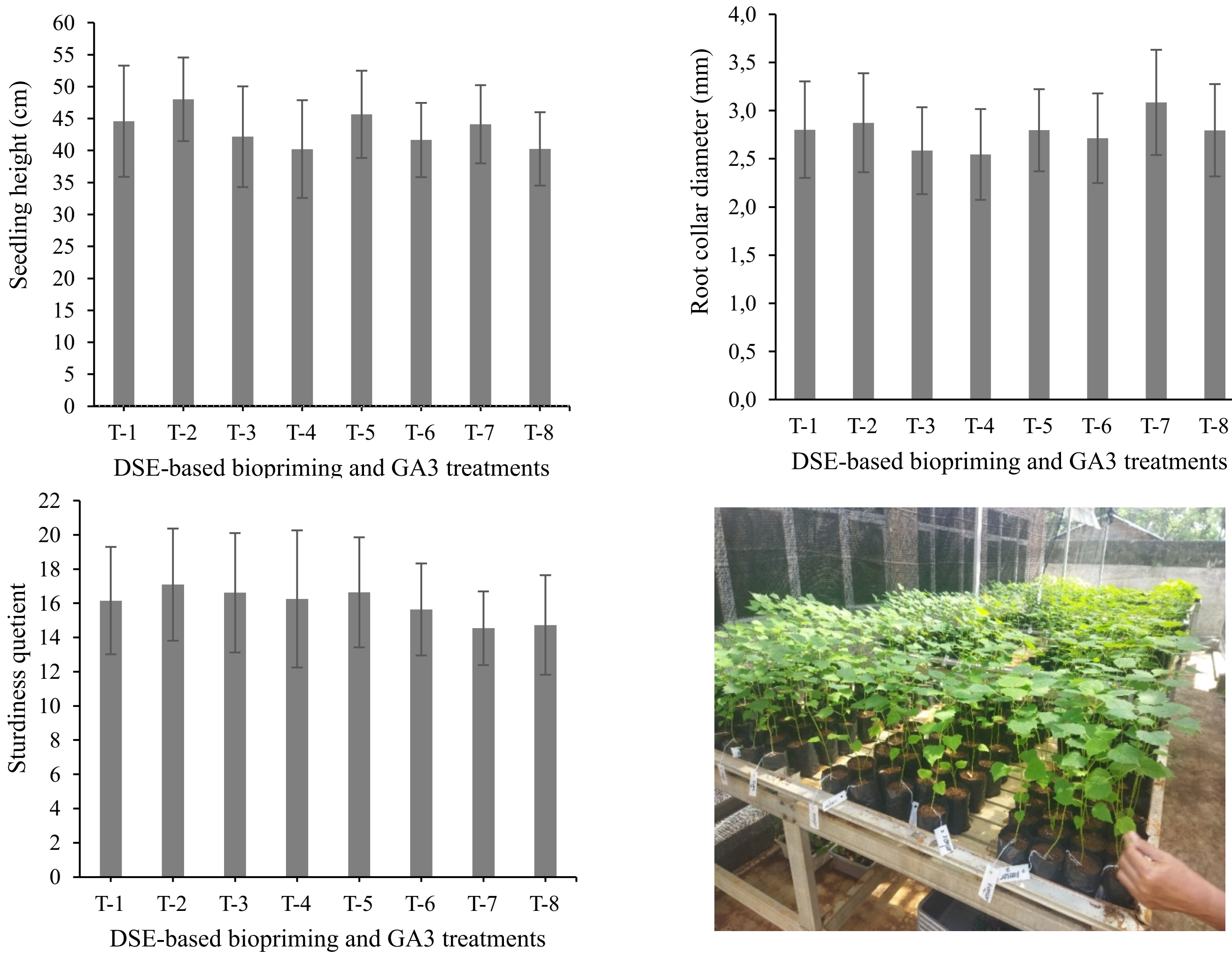

Figure 3 Performance of seedling height, root collar diameter, sturdiness quotient, and seedling lot of *Gmelina arborea* treated by DSE-based biopriming and GA3. Notes: T-0 = control, T-1 = soaking seeds in *C. teunissimum*, T-2 = soaking seeds in *E. pisciphila*, T-3 = soaking seeds in *C. nyingchiensis*, T-4 = soaking seeds in *D. pandanicola*, T-5 = soaking seeds in *Cylindroccarpon* sp., T-6 = soaking seeds in DSE consortium, T-7 = soaking seeds in GA3 250 ppm.

Table 2 Seedling height, root collar diameter, and sturdiness quotient of *Gmelina arborea* treated by DSE-based biopriming and GA3

Seed treatments	Seedling height (cm)	Root collar diameter (mm)	Sturdiness quotient
T-0	44.60 ± 8.71 b	2.80 ± 0.50 b	16.15 ± 3.14 ab
T-1	48.03 ± 6.54 a	2.87 ± 0.51 b	17.10 ± 3.28 a
T-2	42.16 ± 7.88 cd	2.58 ± 0.45 cd	16.62 ± 3.49 ab
T-3	40.23 ± 7.64 d	2.54 ± 0.47 d	16.26 ± 4.01 ab
T-4	40.26 ± 5.73 d	2.80 ± 0.43 b	16.64 ± 3.22 ab
T-5	41.65 ± 5.82 d	2.71 ± 0.46 bc	15.64 ± 2.69 bc
T-6	44.11 ± 6.12 bc	3.08 ± 0.54 a	14.55 ± 2.16 d
T-7	45.66 ± 6.82 b	2.80 ± 0.48 b	14.73 ± 2.90 cd
p-value: Treatment	0.000**	0.000**	0.000**
Block	0.014*	0.136^{ns}	0.618^{ns}

Notes: The same letters following numbers ($\bar{x}$ ± standard deviation)in the same column indicate no significant difference, * = significant at 95% confident level, ** = significant at 99% confident level, ns = no significant, T-0 = control, T-1 = soaking seeds in *C. teunissimum*, T-2 = soaking seeds in *E. pisciphila*, T-3 = soaking seeds in *C. nyingchiensis*, T-4 = soaking seeds in *D. pandanicola*, T-5 = soaking seeds in *Cylindroccarpon* sp., T-6 = soaking seeds in DSE consortium, T-7 = soaking seeds in GA3 250 ppm the control. In general, soaking seeds in a *C. teunissimum* and DSE consortium solution often produced the best growth tendency in terms of seedling height and root collar diameter during the initial growth phase.

Discussion

Priming treatments with DSE and GA3 had a substantial impact on the germination as well as initial growth of G. arborea seedlings. Soaking seeds in *C. teunissimum* solution resulted in the highest increase in *G. arborea* seed viability and vigor (germination rate, germination speed, shoot length, radicle length, mean germination time, and vigor index). Soaking seeds in *C. teunissimum* solution resulted in the highest germination rate (87.25%), followed by soaking seeds in *E. pisciphila* (85.25%) and soaking seeds in DSE consortium (81.25%). The *C. teunissimum* treatment also increased germination rate (44.9%), shoot length (10.9%), mean germination time (13.8%), and vigor index (35.3%) compared to the control. Another treatment to improve seed germination is soaking seeds in the DSE consortium. The effect of DSE biopriming on forest tree species was reported by Deng et al. (2020) on *Pinus sylvestris*, Surono et al. (2024) on *Falcataria moluccana* seeds, and Akhhir et al. (2024) on *P. merkusii*. DSE-*Rhizopycnis vagum* and *Curvularia* sp. associated with *F. moluccana* seeds produce several secondary metabolic compounds, such as antioxidants, antifungals, and antibacterials, which protect seeds from pathogenic disturbances. These compounds include Hexamethyl Cyclotrisiloxane, 1-Isopropenyl-4-methyl-1,3-cyclohexadiene, and Acetamide, 2, 2,2-trifluoro-N-methyl-N- (trimethylsilyl) (Surono et al., 2024). According to Berthelot et al. (2019), DSE can suppress the growth of phytopathogens on plant roots. Furthermore, DSE is known to create growth hormones like Gibberellin (Hamayun et al., 2010), which are required for plant germination and growth (Castro-Camba et al., 2022). Islam (2020) reported using *Cladosporium cladosporioides* to increase rice and wheat germination and vigor index. *Cladosporium* sp. has also been reported to increase tomato plant weight, stem length, and root weight (Răut et al., 2021). In general, several studies of bio-primed seeds have shown rapid germination, uniform seedling emergence, reduced dormancy, and greater tolerance to environmental stress (Ananthi et al., 2014; Singh, 2016).

Soaking *G. arborea* seeds in 250 ppm GA3 has not been able to increase seed germination. In several studies, GA3 improved seed germination of *Eriobotrya japonica* (Al-Hawezy, 2013), *Calopogonium caeruleum* (Asra, 2014), *Cyclamen* spp. (Cornea-Cipcigan et al., 2020), and *Neolamarckia cadamba* (Sudrajat et al., 2022). For *N. cadamba* seeds, soaking seeds in 750 ppm GA3 for 24 hours and 500 ppm GA3 for 48 hours improved seed germination, but soaking seeds in 250 ppm GA3 did not improve it. Hormone availability for germination can be boosted by soaking seeds with GA3 (Al-Hawezy, 2013; Miransari & Smith, 2014). However, in this study, soaking *G. arborea* seeds in 250 ppm GA3 was suspected to be suboptimal, as reported in previous research conducted by Iskandar et al. (2020). Koryzniene et al. (2019) reported a study of GA3 application on *Heracleum sosnowskyi* seeds, which showed a decrease in germination capacity from 98.0% (control) to 16.5% (GA3 concentration 0.43 mM). According to Rout et al. (2021), the optimal GA3 dose for *Saraca asoca* seeds is 200 ppm; doses below or above this tend to result in lower germination. This illustrates that the GA3 application requires an appropriate dose and soaking time to achieve optimal results.

DSE may have an ecological role similar to mycorrhiza (Ruotsalainen et al., 2021). They can increase the uptake of mineral nutrients by host plants (Wu et al., 2021) and improve host resistance to biological and abiotic stresses (Wen et al., 2021; Qu et al., 2022). Wang et al. (2022) reported that inoculation of the *Medicago sativa* rhizosphere with DSE extracellular metabolites promoted nutrient uptake, plant growth, and biomass. DSEs are endophytic fungi with a "facultative-saprotrophic" character, which are able to mineralize organic nutrient sources (N and P) and increase nutrient acquisition as a decomposer of soil organic compounds as well as a promoter of host plant seedling growth (Surono & Narisawa, 2017; Malicka et al., 2022; Luo et al. 2023). DSE inoculation can enhance soil enzyme activity, increase soil nutrient content, and stimulate plant hormone production pathways (Shi et al., 2025). DSEs are reported to be able to synthesize or modulate phytohormones such as IAA, gibberellins, and cytokinins that stimulate cell elongation, lateral root formation, and the transition from the imbibition phase to early growth (Baron & Rigobelo, 2021; Huertas et al., 2024; Silva et al., 2024; Surono et al., 2024; Yuniarti et al., 2025). Hormones play a crucial role in regulating plant metabolism and promoting plant growth, and endophytic fungi are involved in regulating the hormone levels of the host plant (Sharma et al., 2023).

DSEs have the potential to increase the tolerance of host plants to drought, salinity, and heavy metal stress through melanin/antioxidant-based mechanisms, root architectural restructuring, and heavy metal sequestration (Santos et al., 2021; Marfuah et al., 2024; Septian et al., 2025). According to Pang et al. (2020), DSE inoculation can increase pathways and gene expression related to plant stress resistance. Lu et al. 2025 reported that inoculation of DSE (*Gaeumannomyces hyphopodioides*) on *Ammopiptanthus mongolicus* (Leguminosae) can reduce drought stress damage by increasing CAT activity, AsA content, and soluble sugar content in roots, with a significant reduction of MDA accumulation by 97.7%. *G. hyphopodioides* also significantly increased the content of zeatin and brassinosteroid, which in turn regulated root structure and increased root activity, resulting in a 208.6% increase in root biomass (Lu et al., 2025). DSE can also protect seeds/seedlings from seed-borne/soil-borne pathogens through competition for space/nutrients, antibiosis, and/or induction of resistance, such as the DSE species *Phialocephala fortinii* is reported to inhibit Fusarium in asparagus (Surono & Narisawa, 2018), and application of DSE in the nursery phase suppresses *Rigidoporus microporus* (white root rot) in rubber seedlings (Dalimunthe et al., 2023).

Soaking seeds in *C. teunissimum* can also increase seedling height growth, while soaking seeds in a DSE consortium solution provides the highest diameter growth. Several previous studies have demonstrated that DSE can enhance the growth of *P. sylvestris* (Alberton et al., 2010; Deng et al., 2020), *P. merkusii* (Akhir et al., 2024), and *Agathis borneensis* seedlings (Yuniarti et al., 2025). In *P. merkusii*, DSE can increase organic carbon content and seedling nutrient uptake (Akhir et al., 2024). Andrade-Linares et al. (2011) and Surono & Narisawa (2017) argue that DSE is a mutualistic endophytic fungus characterized by septate hyphae containing melanin, exhibiting black pigmentation, and forming microsclerotia within the root tissue of host plants, hence enhancing the growth and production of several plant species without inducing pathology. However, some DSE treatments in this study provided height growth below the control. The same thing happened with seed diameter; some DSE provided significant diameter growth below the control, such as soaking seeds in *E. pisciphila, C. nyingchiensis,* and *Cylindroccarpon* sp. Azmi et al. (2022) reported that not all DSE strains had a positive effect on the growth of *Allium ascalonicum* when compared to the control. According to Li et al. (2019), plant responses to DSE inoculation vary from neutral to beneficial, depending on the plant and fungal species. For example, two of the three DSEs improved root growth in *Hedysarum scoparium* under both mild and extreme drought conditions. The soil environment will also influence DSE colonization (Hou et al., 2019; Sudová et al., 2020). In this study, *C. teunissimum* is thought to be compatible with the host plant (*G. arborea*). The DSE consortium also has a positive effect on growth, especially *G. arborea* seedling diameter. Inoculation with the DSE consortium allows interactions with other members of the DSE community in the roots, which may also influence DSE colonization success (Wang et al., 2025). The same thing was also reported by Suita et al. (2024) in *Pongamia pinnata*. Other studies have shown the presence of DSE-produced inhibitors such as Benzoic Acid (El-Mohamedy et al., 2015; Azmi et al., 2022). El-Mohamedy (2015) reported that soaking seeds in synthetic benzoic acid did not markedly enhance the growth and pod yield of green beans, including plant height, branch number, leaf number, wet and dry leaf weight, pod quantity and weight, and overall pod yield. In this study, soaking seeds in *C. teunissimum* produced the highest sturdiness index. Height growth was faster because the conditions of the seedlings grown in the nursery were too dense, resulting in a relatively small diameter and a high sturdiness quotient value. Seeds with a sturdiness quotient that is too high indicate their susceptibility to physical damage during planting (Budiman et al., 2015). Roller (1977) found that *Picea mariana* seedlings with a sturdiness quotient of more than 6 are highly susceptible to damage when exposed to wind and drought. Therefore, the next step in seedling hardening is placing the seedlings in an open area and widening the distance between them to stimulate diameter growth and stem movement, thus increasing the sturdiness index (Nurhasybi et al., 2019).

Consistent with our findings, international studies have shown that DSE inoculation can improve early performance of various tree species by improving nutrient acquisition and N-use efficiency of *P. sylvestris* under N limitation and high CO_2) (Alberton et al., 2010), as well as suppressing damping-off disease while improving rhizosphere conditions in *P. sylvestris* var. mongolica (Deng et al., 2020). In the context of heavy metal stress, DSE (alone or in combination with ectomycorrhizae) has also been reported to improve tolerance and growth of *Pinus tabulaeformis* under Cd stress (Zhou et al., 2024), consistent with physiological evidence that DSE is capable of producing growth-promoting metabolites and contributing to heavy metal tolerance (Berthelot et al., 2016) and that its benefits tend to be most pronounced under both biotic and abiotic stress conditions (Malicka et al., 2022). DSE accelerates germination and increases the vigor of *F. moluccana* seeds and triggers the accumulation of potentially protective secondary metabolites (Surono et al., 2024), improves the morphophysiological properties of *N. cadamba* seedlings (Putri et al., 2025), and is effective as biopriming to improve seed quality and the growth of *A. borneensis* seedlings (Yuniarti et al., 2025) and *Pongamia pinnata* seedlings (Suita et al., 2024). Furthermore, in extreme ecosystems such as gold mine tailings, DSE inoculation increased Pb phytoremediation and the performance of two bioenergy tree species, namely *Jatropha curcas* and *Reutealis trisperma* (Marfuah et al., 2024), strengthening the suspicion that the DSE mechanism works in a multipathway–from nutrient mobilization (including P solubilization) (Surono & Narisawa, 2017; Luo et al., 2023) to hormone/antioxidant modulation and protection against pathogens/abiotic stress (Dalimunthe et al., 2023).

The seed soaking treatment in DSE can be categorized as a biopriming treatment. Rakshit et al. (2015) and Dhawal et al. (2016) stated that bio-priming is a seed treatment technique that combines biological and physiological aspects of improving seed viability, vigor, and plant growth. The process is achieved by seed hydration and microbial coating on the seeds using beneficial biological agents (Ananthi et al., 2014). Sarkar et al. (2017) and Devika et al. (2021) suggested that the amount used to maintain seed moisture potential and soaking duration controls seed metabolism and promotes the seeds' pre-germination processes (cell repair and protein synthesis). Bio-priming can activate plant cellular mechanisms, reconfigure metabolism, and enhance plant growth (Singh et al., 2016; Sarkar et al., 2017). In this study, DSE treatment highly depends on the seed type or species, DSE strain, germination conditions, and seed treatment (soaking time). Several studies reported the ineffectiveness of DSE treatment in increasing seed germination, such as in *A. ascalonicum* (Azmi et al., 2022) and *P. pinnata* (Suita et al., 2024), but the treatment can increase seedling growth. However, in this study, the opposite occurred; several DSE strains, such as *E. pisciphila, C. nyingchiensis, D. pandanicola*, and *Cylindroccarpon* sp., provided height and diameter growth below the control or negatively affected the initial growth of *G. arborea* seedlings, although they had a positive effect on germination and germination rate.

Generally, the seeds used were those that had been stored for one year. They were still relatively good with a germination capacity of 72.25% (control) and still in accordance with the quality standards for seeds suitable for distribution (germination capacity $\geq$ 70%) as stated in SNI (Indonesian National Standard) 7627:2022 Physical and physiological quality of forest tree seed (Badan Standardisasi Nasional, 2022). The soaking of seeds in *C. teunissimum* solution yielded the highest germination rate (87.25%), representing an improvement of 20.76% over the control (without treatment). For seedling quality, the seedling height ranging from 40.26 to 48.03 cm has met the seedling quality standards according to SNI 8420:2018 Forest tree seedling, but the diameter has not met the standard (≥ 4) (Badan Standardisasi Nasional, 2018). Root collar diameter ranges from 2.54 (DSE-*C. nyingchiensis* treatment) to 3.08 mm (DSE consortium treatment). The seedling diameter standard has not been achieved because the seedlings are still 2 months old in the nursery (shading area) and have not yet undergone the hardening-off stage (placing the seedlings in an open area with the distance between the seedlings widened), which generally allows the stem to enlarge and strengthen. Planting fast-growing tree seedlings, such as G. arborea, is typically done after the seedlings are 3 months old (Nurhasybi et al., 2019). In general, seeds soaked in *C. teunissimum* and DSE consortium solutions exhibited better germination and seedling growth than those in other treatments. Thus, selecting the appropriate treatment is essential to determine the optimal DSE strain and soaking treatment for achieving optimal seed germination and seedling growth.

In field applications, the effects of DSE have the potential to persist post-transplantation if colonization is established during the seed-seedling stage (e.g., biopriming/seed soaking), as DSE can penetrate early tissues and maintain endophytic relationships during the seedling stage. However, its persistence depends on isolate-host compatibility, site conditions, and local microbial competition. Therefore, practical strategies often emphasize early inoculation plus reinforcement in the nursery (e.g., reapplication via media/watering) to maintain colonization until outplanting (Surono et al., 2024; Malicka et al., 2022). DSE inoculum needs to be formulated (solid or liquid carrier) with controlled moisture content, storage temperature, and viability protection agents; QA/QC (viability/purity testing) practices are key because decreased viability during storage will reduce the consistency of seedling response (Chaudhary et al., 2020). The main challenges of scale-up for commercial use in nurseries typically include standardization of propagule density, contamination control, product stability during distribution, and consistency of performance across batches, which are common issues with microbial bioformulation technologies and require stringent production SOPs and multi-site efficacy testing (Khan et al., 2023). Regarding compatibility with nursery protocols, DSE is relatively easy to integrate through seed treatment (soaking/priming), incorporation into seedling media, or drench/irrigation, but attention must be paid to practices that potentially suppress pathogenic fungi and synchronization with other existing seed treatment technologies. Examples of operational seed treatment-based implementations in nurseries are shown in the combination of treatments (including DSE) that affect seedling performance in nursery systems (Suita et al., 2024; Marfuah et al., 2024; Septian et al., 2025).

Conclusion

The treatment of soaking seeds in *C. teunissimum* and DSE consortium provided better germination and seedling growth than other treatments. Soaking seeds in *C. teunissimum* solution gave the highest germination rate (87.25%), followed by soaking seeds in *E. pisciphila* (85.25%) and soaking seeds in DSE consortium (81.25%). The *C. teunissimum* treatment also increased germination rate (44.9%), shoot length (10.9%), mean germination time (13.8%), and vigor index (35.3%) compared to the control. The DSE treatment that consistently had a positive effect on *G. arborea* seed germination compared to the control, especially for the parameters of germination capacity, germination speed, shoot length, mean germination time, and vigor index, was soaking seeds in *C. teunissimum* and the DSE consortium. Soaking seeds in *C. teunissimum* also produced the highest seedling height, 48.60 cm (an increase of 7.6% from the control). In contrast, the DSE consortium produced the highest seedling diameter, 3.08 mm (an increase of 10.7% from the control). Thus, the application of *C. teunissimum* and DSE consortium to improve the quality of *G. arborea* seeds and seedlings has promising potential.

Recommendation

Providing high-quality seeds and seedlings is essential for developing plantation and community forests and rehabilitating degraded forests and lands. The results of this study recommend using dark septate endophyte-based biofertilizers, which are still rarely used in forest development in Indonesia, especially for *G. arborea*. This research suggests that the treatment of seed soaking in *C. teunissimum* solution and DSE consortium can be applied in the development of *G. arborea* seedlings. Those treatments produce the best viability (germination) and seedling growth possible, and can be applied in the development of sustainable management of plantation and community forests. For DSE biopriming in nurseries, prepare pure DSE cultures (e.g., in PDA/PDB) and then increase the biomass and/or propagule suspension; perform quality control with viability tests (regrowth/reisolation on media) and contaminant screening before inoculum formulation (Chaudhary et al., 2020; Khan et al., 2023). Seed treatment can be carried out by standardized soaking: for *P. pinnata* seedlings, a 0.1% DSE suspension was used for 24 hours and was reported to increase seedling growth (Suita et al., 2024), while for *A. borneensis*, biopriming with DSE for 6 hours effectively increased seedling vigor and quality parameters when initial seed viability was still adequate (Yuniarti et al., 2025). After soaking, drain and air-dry briefly, sow in sterile media, and if necessary, store the treated seeds under controlled cool-humid conditions. For distribution, the inoculum should be formulated in a carrier that maintains stability and shelf life (Chaudhary et al., 2020; Khan et al., 2023). Success is monitored through accelerated/increased germination, improved seedling quality index, and evidence of early colonization and functional DSE responses in forestry tree species–for example, colonization/metabolite activity detected as early as 23 hours in *F. moluccana* (Surono et al.,

2024) and improved seedling morphophysiological traits in *N. cadamba* (Putri et al., 2025).

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