

Allelopathic Effects of Aqueous Extract of Metasequoia Litter on Its Seed Germination and Growth: Postprint

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Abstract

To investigate whether the allelopathic effects of *Metasequoia glyptostroboides* litter constitute an obstacle to its natural regeneration, this study established eight concentrations (200, 100, 50, 20, 10, 5, 2, 1 g · L⁻¹) of aqueous extracts from both fresh and naturally decomposed *M. glyptostroboides* litter, plus a control (CK), to analyze the effects of different types and concentrations of litter aqueous extracts on the allelopathic impacts on seed germination and growth of *M. glyptostroboides*. The results showed: (1) The aqueous extract of fresh *M. glyptostroboides* litter had no significant effect on seed germination rate and germination potential ($P > 0.05$), but had a significant effect on germination index ($P < 0.05$), with 1, 100, and 200 g · L⁻¹ significantly inhibiting seed germination. Although the aqueous extract of naturally decomposed *M. glyptostroboides* litter had no significant effect on all three seed germination indicators ($P > 0.05$), inhibitory effects were observed at concentrations of 5, 10, 50, and 200 g · L⁻¹. (2) The bud length, hypocotyl length, and main root length of *M. glyptostroboides* seeds all differed significantly among different concentrations of both fresh and naturally decomposed litter aqueous extracts ($P < 0.05$), and gradually decreased with increasing extract concentration (10 g · L⁻¹), with the inhibitory effect being particularly enhanced within the 50–200 g · L⁻¹ range. (3) The inhibitory effects of both fresh and naturally decomposed *M. glyptostroboides* litter aqueous extracts on seed germination and seedling growth were stronger than those on seed germination, and the inhibitory intensity of allelopathy shaped growth curve ($R^2 = 0.988$). *M. glyptostroboides* litter exerts certain allelopathic inhibitory effects on its own seed germination and growth, affecting natural regeneration of its populations. It is recommended that in the management of *M. glyptostroboides* populations, understory litter should be appropriately cleared to promote natural regeneration of *M. glyptostroboides* populations.

Full Text

Allelopathy of Aqueous Extract from *Metasequoia glyptostroboides* Litter on Its Seed Germination and Growth

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Abstract

To explore whether the allelopathy of *Metasequoia glyptostroboides* litter constitutes an obstacle to its natural regeneration, we established eight concentrations (200, 100, 50, 20, 10, 5, 2, 1 g · L⁻¹ and a control) of aqueous extracts from both fresh and naturally decomposed litter to analyze their allelopathic effects on seed germination and growth. The results revealed: (1) Fresh litter aqueous extract had no significant effect on seed germination rate or germination potential (P>0.05), but significantly affected germination index (P<0.05), with 1, 100, and 200 g · L⁻¹ treatments significantly inhibiting germination. Although natural litter aqueous extract showed no significant effects on the three germination metrics (P>0.05), inhibitory effects were observed at concentrations of 5, 10, 50, and 200 g · L⁻¹. (2) Shoot length, hypocotyl length, and primary root length differed significantly across concentrations of both fresh and natural litter extracts (P<0.05), decreasing gradually with increasing extract concentration (10 g · L⁻¹), particularly showing significantly enhanced inhibition in the 50–200 g · L⁻¹ range. (3) Both fresh and natural litter extracts exhibited stronger inhibitory effects on post-germination growth than on germination itself, with fresh litter showing stronger allelopathic inhibition than natural litter. (4) Among all germination and growth indices, primary root length was the most sensitive to allelochemicals. (5) The dynamic growth of shoot length followed an “S”-shaped growth curve (R² 0.988). *M. glyptostroboides* litter exerts certain allelopathic inhibitory effects on its own seed germination and growth, thereby affecting natural population regeneration. We recommend appropriate removal of understory litter in *M. glyptostroboides* population management to promote natural regeneration.

Keywords: *Metasequoia glyptostroboides*, litter, natural regeneration, allelopathy, autotoxicity, aqueous extracts

Allelochemicals are primarily water-soluble substances released into the environment through plant decomposition, rhizosphere secretion, rainwater leaching, and volatilization (Rice, 1984; Kimura et al., 2015). Litter represents one of the most important sources of allelochemicals in forest trees, as its decomposition releases inherent substances or transforms them into secondary compounds that affect seed germination and seedling growth, thereby becoming a key factor ob-

structuring natural forest regeneration (Caviers et al., 2007; Muturi et al., 2017; Aguilera et al., 2017). The concentration effects of litter allelopathy primarily manifest as dual “low-promotion, high-inhibition” effects on plant seed germination and seedling growth (Li et al., 2010; Zhuang et al., 2017), or as “inhibitory effects” that intensify with increasing concentration, consequently creating barriers to natural regeneration (Zhang et al., 2016; Guo et al., 2019). Different plant parts and decomposition stages also produce varying allelopathic effects (Fernandez et al., 2006; Huang et al., 2019).

Metasequoia glyptostroboides, a relict species in the family Cupressaceae and genus *Metasequoia*, is a “living fossil” endemic to China and a nationally protected first-class tree species. Existing native parent trees are distributed only within a narrow triangular region between Lichuan City in Hubei Province, Longshan County in Hunan Province, and Shizhu County in Chongqing Municipality, totaling merely 5,696 individuals. Natural regeneration of *M. glyptostroboides* seedlings and saplings is rarely observed in the understory of native parent trees or in 35–42-year-old clonal seed orchards established at the Lichuan Mother Tree Management Station and Lichuan Forestry Science Institute (Lin et al., 2017). This phenomenon has attracted considerable academic attention to the barriers and breeding mechanisms of *M. glyptostroboides* natural regeneration. Researchers have explored various aspects including growth environment and disturbance (Hu and Zheng, 1948; Lin et al., 2017; Chen et al., 2020), population and genetic structure (Huang et al., 2020; Liu, 2020), and mating and dispersal patterns (Chen, 2016). Additionally, numerous studies have investigated regeneration breeding, examining effects of individual parent trees and seed provenance differences (Wu et al., 2020), temperature (Xin et al., 2004), light (Guo et al., 2018), water (Fan et al., 2020), selenium (Guo et al., 2018), and soil covering after sowing (Li et al., 2012) on seed germination. However, the mechanisms underlying difficult natural regeneration remain incompletely understood.

Field surveys of major *M. glyptostroboides* distribution areas revealed substantial litter accumulation beneath the canopy, with only occasional individual seedlings observed. Natural regeneration of woody plant populations represents a crucial process for population perpetuation and expansion under natural forces, with seed germination and early seedling establishment being the two most critical stages—both significantly influenced by allelopathic effects from understory litter (Aliskan and Terzi, 2015). Moreover, allelopathic effects vary across different regeneration stages as the released allelochemical composition changes (Fernandez et al., 2008). This study investigated whether allelopathic effects from accumulated litter around *M. glyptostroboides* parent trees constitute a barrier to natural regeneration by testing different concentrations of aqueous extracts from two litter types on seed germination, providing scientific evidence to elucidate the obstacles to natural regeneration.

1.1 Seed and Litter Collection and Processing

Experimental seeds were collected in November 2020 from *M. glyptostrobooides* native parent tree No. 1076 (118 years old, 31 m height, 87.6 cm DBH, located at 108°35 45.1 E, 30°07 20.5 N, 1,114 m elevation). Seed moisture content was $9.78\% \pm 1.13\%$, with a thousand-seed weight of 2.57 ± 0.17 g.

To ensure representative litter collection, 30 collection frames were randomly deployed across five directional zones (east, south, west, north, and center) in the *M. glyptostrobooides* seed orchard at the Lichuan Forestry Science Institute. Fresh litter (naturally abscised current-season litter not yet undergoing decomposition, including mixed leaves, branches, fruits, and bark) was collected in late October 2020, while natural litter (surface litter including undecomposed, semi-decomposed, and fully decomposed mixtures of leaves, branches, and fruit peels) was collected in late November 2020. All collected litter was air-dried at room temperature before subsequent processing.

1.2.1 Preparation of Litter Aqueous Extracts

Fresh and natural litter samples were air-dried, pulverized (passed through 100-mesh sieve), and mixed with distilled water at a solid-liquid ratio of 1:5. The mixture was shaken at room temperature for 48 hours, then centrifuged at $10,000 \text{ r} \cdot \text{min}^{-1}$ for 10 minutes. The supernatant constituted the $200 \text{ g} \cdot \text{L}^{-1}$ stock solution, designated as fresh litter extract (FL) and natural litter extract (NL), respectively. All extracts were stored at $-18 \text{ }^{\circ}\text{C}$.

1.2.2 Seed Germination and Growth Experiments

Both FL and NL were diluted to eight concentrations: 200, 100, 50, 20, 10, 5, 2, and $1 \text{ g} \cdot \text{L}^{-1}$, with distilled water as control (CK), totaling 17 treatments with three replicates each. Fifty plump, uniform seeds were evenly distributed in petri dishes (Φ 9 cm, sterilized at $180 \text{ }^{\circ}\text{C}$ for 2 hours) lined with two layers of filter paper. Each dish received 4 mL of the corresponding extract solution and was incubated at $20 \text{ }^{\circ}\text{C}$ (based on the average April-May temperature in Lichuan from the National Meteorological Science Data Center) in complete darkness (Xin et al., 2004; Guo et al., 2018) using an SPX-30085H-II biochemical incubator. Filter papers were replaced and 4 mL of corresponding solution was added every three days to maintain consistent extract concentration. Germination was monitored every 24 hours from the start of the experiment, with radicle emergence as the germination criterion. After germination, 10 seedlings were randomly selected from each replicate to measure shoot length, recorded periodically until germination was complete. Approximately 20 days later, hypocotyl length (distance from cotyledon attachment point to primary root) and primary root length (root developed from radicle) were measured (Qiang, 2005). Germination rate, germination potential, and germination index were calculated from germination data. Allelopathic effect sensitivity index and comprehensive allelopathic effect index were calculated based on seed germination and shoot/root

growth using the following formulas:

- (1) Germination rate:

$$\text{Germination rate} = \frac{G_a}{G_t} \times 100\%$$

where G_a is the number of normally germinated seeds and G_t is the total number of tested seeds.

- (2) Germination potential:

$$\text{Germination potential} = \frac{G_{\max}}{G_t} \times 100\%$$

where G_{\max} is the number of germinated seeds on the day with maximum germination.

- (3) Germination index:

$$\text{Germination index} = \sum \frac{G_p}{G_d}$$

where G_p is the number of seeds germinated on day d and G_d is the number of days.

- (4) Allelopathic effect sensitivity index (Williamson & Richardson, 1988):

$$RI = \begin{cases} \frac{C-T}{C} & \text{if } T \geq C \\ \frac{T-C}{C} & \text{if } T < C \end{cases}$$

where RI is the allelopathic effect sensitivity index, C is the control value, and T is the treatment value. $RI > 0$ indicates promotion, $RI < 0$ indicates inhibition, and the absolute value of RI reflects the intensity of the effect.

- (5) Comprehensive allelopathic effect index (SE), reflecting overall allelopathic strength, is the arithmetic mean of RI values for all tested parameters under the same treatment:

$$SE = \frac{RI_{\text{germination rate}} + RI_{\text{germination potential}} + RI_{\text{germination index}} + RI_{\text{shoot length}} + RI_{\text{hypocotyl}} + RI_{\text{prim}}}{6}$$

1.2.3 Data Processing

Variance analysis and multiple comparisons (Duncan) were performed on seed germination and growth under different FL and NL concentrations. SPSS 18.0 software was used for Logistic model fitting and growth parameter calculation of shoot length growth dynamics under different treatments (Yang et al., 2011; Wu et al., 2020), including maximum linear growth rate (MGR, growth rate

at maximum daily increment), linear growth rate (LGR, average growth rate during linear growth period), total linear growth (TLG, growth amount during linear growth period), and percentage of linear growth relative to total growth. The formulas are as follows.

Logistic model fitting equation:

[Equation corrupted in original]

where y is cumulative shoot length, k represents the asymptotic maximum shoot length, t is growth time, and a and b are coefficients to be determined.

2.1 Effects of Litter Extracts on Seed Germination

As shown in [Figure 1: see original paper], different litter extracts produced varying effects on seed germination indices. Fresh litter extract (FL) significantly affected germination index ($P < 0.05$) but not germination rate or germination potential ($P > 0.05$). Under FL treatment, germination rate, germination potential, and germination index showed fluctuating patterns with increasing concentration, peaking at $50 \text{ g} \cdot \text{L}^{-1}$ but showing significant inhibition at $1 \text{ g} \cdot \text{L}^{-1}$ (germination rate and index reduced by 36.842% and 32.677% compared to CK, respectively). Natural litter extract (NL) showed no significant effects on the three germination metrics ($P > 0.05$), though germination rate, potential, and index were higher than CK at $1 \text{ g} \cdot \text{L}^{-1}$, with germination potential (36.000%) being 2.349 times higher than at $10 \text{ g} \cdot \text{L}^{-1}$. Overall, FL at $50 \text{ g} \cdot \text{L}^{-1}$ slightly promoted germination, while 1, 100, and $200 \text{ g} \cdot \text{L}^{-1}$ were inhibitory. NL showed promotional effects at $1 \text{ g} \cdot \text{L}^{-1}$ but inhibitory effects at 5, 10, and $200 \text{ g} \cdot \text{L}^{-1}$.

2.2.1 Effects on Three Seed Growth Indicators

As illustrated in [Figure 2: see original paper], FL concentration significantly affected shoot length, hypocotyl length, and primary root length ($P < 0.01$), with all treated values below CK. Inhibition intensified with concentrations above $10 \text{ g} \cdot \text{L}^{-1}$, while lower concentrations caused fluctuating responses. NL concentration significantly affected shoot and primary root length ($P < 0.01$) and hypocotyl length ($P < 0.05$), with maximum values observed in CK (45.000, 11.767, and 28.867 mm, respectively), followed by $10 \text{ g} \cdot \text{L}^{-1}$. Growth indicators decreased progressively with concentrations above $10 \text{ g} \cdot \text{L}^{-1}$. In the 1–5 $\text{g} \cdot \text{L}^{-1}$ range, shoot and hypocotyl lengths declined gradually, while primary root length first decreased then increased, demonstrating concentration-dependent inhibition. Both FL and NL extracts inhibited post-germination growth, with particularly significant inhibition at concentrations exceeding $20 \text{ g} \cdot \text{L}^{-1}$.

2.2.2 Effects on Bud Growth Process

Shoot length growth exhibited a pattern of initial slow growth, followed by rapid growth, then slowing until cessation, conforming to an “S”-shaped growth curve. Logistic model fitting yielded determination coefficients of 0.988–0.998 for both FL and NL treatments, all reaching extremely significant correlation levels. As extract concentration increased, the shoot growth curve became flatter and the linear growth phase commenced later ([Figure 3: see original paper]). At 100 and 200 $\text{g} \cdot \text{L}^{-1}$, FL produced markedly lower growth curves than NL, indicating more pronounced inhibition of shoot growth progression at high concentrations.

As shown in , both FL and NL treatments caused gradual declines in MGR and LGR with increasing concentration. Values were higher than CK at 1–5 $\text{g} \cdot \text{L}^{-1}$ but fell below CK at concentrations $50 \text{g} \cdot \text{L}^{-1}$. TLR values were all lower than CK and, except for 2 and 5 $\text{g} \cdot \text{L}^{-1}$ treatments, decreased progressively with concentration. Linear growth accounted for 55.263%–64.683% of total growth.

2.3 Evaluation of Allelopathic Effects

As presented in , FL treatment produced negative RI values for germination indices at 1–5 $\text{g} \cdot \text{L}^{-1}$ and 100–200 $\text{g} \cdot \text{L}^{-1}$, indicating inhibition. The strongest inhibition on germination rate and potential occurred at 1 $\text{g} \cdot \text{L}^{-1}$, while 200 $\text{g} \cdot \text{L}^{-1}$ most strongly inhibited germination index. Non-significant promotion occurred at 10–50 $\text{g} \cdot \text{L}^{-1}$. NL treatment showed positive RI values at 1–2 $\text{g} \cdot \text{L}^{-1}$ (promotional effects), with inhibitory effects becoming more pronounced at higher concentrations. Both FL and NL inhibited shoot length, hypocotyl length, and primary root length, with inhibition strengthening at concentrations $10 \text{g} \cdot \text{L}^{-1}$. Primary root length showed greater sensitivity than hypocotyl or shoot length.

The comprehensive allelopathic effect index (SE) revealed that all FL concentrations inhibited seed germination and growth (range: -0.001 to -0.562), with inhibition decreasing at 1–10 $\text{g} \cdot \text{L}^{-1}$, fluctuating at 10–50 $\text{g} \cdot \text{L}^{-1}$, and peaking at 100–200 $\text{g} \cdot \text{L}^{-1}$. NL exhibited a “low-promotion, high-inhibition” dual effect, with slight promotion at 1 $\text{g} \cdot \text{L}^{-1}$ (SE = 0.044) and increasingly strong inhibition at higher concentrations. Overall, FL demonstrated stronger inhibitory effects than NL, with concentration-dependent variation in inhibition intensity.

Discussion and Conclusion

Seed germination represents a critical life history stage significantly influenced by litter allelopathic effects, thereby affecting population establishment and regeneration (Liu et al., 2017). This study confirms that *M. glyptostroboides* litter exerts inhibitory effects on its own seed germination and growth, indicating that parent tree litter poses an allelopathic barrier to natural regeneration. Fresh litter extract at extremely low concentration (1 $\text{g} \cdot \text{L}^{-1}$) hindered germination, consistent with Macias (1995), likely because fresh litter contains allelochemicals

such as naphthalenes, esters, and alcohols that interfere with seed metabolism, inhibit cell division and elongation, and affect membrane permeability. The specific active compounds require further investigation. High concentrations ($100, 200 \text{ g} \cdot \text{L}^{-1}$) of fresh litter extract also inhibited germination and growth, aligning with Jin et al. (2020) who reported that high concentrations of *Castanopsis kawakamii* undecomposed layer extract inhibited *Cunninghamia lanceolata* seed germination. This occurs because high concentrations of allelochemicals accumulate to levels that damage cellular organelles (Mahdavi et al., 2017), impairing water and mineral uptake and consequently restricting germination and growth.

Natural litter extract showed no significant effects on germination rate, potential, or index, yet exhibited inhibitory effects at all concentrations except $1 \text{ g} \cdot \text{L}^{-1}$, where slight promotion occurred. High concentrations also delayed germination timing. Garnett et al. (2004) similarly found that litter from three dominant tree species in New Jersey had no effect on pitch pine germination, primarily because natural litter's allelochemical activity is reduced by microbial decomposition, weathering, and leaching (Araniti et al., 2016), consequently diminishing allelopathic effects.

The seedling stage is crucial in plant life history, and the shoot represents the initial phase of early seedling establishment, influenced by numerous factors (Lin et al., 2011). Both fresh and natural litter extracts inhibited shoot, hypocotyl, and primary root length, particularly at concentrations exceeding $20 \text{ g} \cdot \text{L}^{-1}$, consistent with findings on *Toona ciliata* var. *pubescens* leaf litter autotoxicity (Guo et al., 2019). Litter-released allelochemicals can damage root tissues, inhibit root hair formation (Aguilera et al., 2017), reduce water and nutrient absorption, and hinder organic matter accumulation, thereby significantly suppressing seedling growth and ultimately affecting survival and competitive ability in the population, which hinders natural regeneration. Primary root length showed greater sensitivity than hypocotyl and shoot length, corroborating Chon et al. (2002) who reported that alfalfa roots were more sensitive to autotoxic allelochemicals than germination rate or hypocotyl length. Since the primary root directly absorbs energy for growth, it is the first and most significantly affected organ (Zhang et al., 2013).

The "S"-shaped growth curve describes population growth under spatial constraints (Lu et al., 2002). This study found that *M. glyptostrobooides* shoot growth dynamics followed an "S"-shaped curve ($R^2 = 0.988$), with low concentrations ($20 \text{ g} \cdot \text{L}^{-1}$) slightly promoting growth rate while medium-high concentrations were inhibitory. This concentration-dependency arises because low concentrations induce tolerance proteins and rapid growth to cope with stress, whereas concentrations exceeding the plant's self-regulation threshold cause increasingly apparent inhibition (Craine and Dybzinski, 2013). Furthermore, linear growth during the experimental period accounted for over 55% of total growth, confirming that the linear growth phase is a critical period for *M. glyptostrobooides* development regardless of conditions

(Wu et al., 2020).

The allelopathic effect sensitivity index is an important metric for allelopathic intensity. This study found that litter extracts affected post-germination growth more than germination itself, because shoots have direct and prolonged contact with allelochemicals, while seed coats and wings provide protective lag in response (Devaney et al., 2018). Different litter types and concentrations produce varying effects, with the comprehensive index showing that fresh litter extract had stronger inhibitory effects than natural litter extract, consistent with Guo et al. (2018) and Liu et al. (2017). This likely reflects differences in allelochemical composition and content across decomposition stages. However, these results were obtained under laboratory conditions and require field validation. Moreover, natural regeneration is influenced by complex environmental factors (temperature, light, water, litter), anthropogenic factors (seed collection, disturbance), and species characteristics (seed viability, provenance, reproductive traits, genetic structure), necessitating comprehensive research to effectively promote natural regeneration.

Seed germination and early growth are vital stages for natural regeneration. This study demonstrates that both fresh and natural *M. glyptostrobooides* litter aqueous extracts produce allelopathic effects, generally inhibitory, confirming that litter allelopathy constitutes a barrier to natural regeneration. Since *M. glyptostrobooides* sheds litter around the time of cone maturation, we recommend timely understory litter removal before the peak seed rain period in future conservation and breeding management to prevent allelochemical accumulation and create favorable conditions for seed germination and seedling growth, thereby promoting natural population regeneration.

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