

Article

Is Soil Covered with *Climacium dendroides* More Conducive to the Germination of *Pinus koraiensis* Seeds?

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Abstract: Our previous investigation has indicated that the natural regeneration of *Pinus koraiensis* occurs solely in soil covered by *Climacium dendroides*. This study aimed to determine whether *C. dendroides*-covered soil enhances seed germination or reduces seed decay. The experiment was divided into two parts: a simulated natural regeneration field experiment, and a greenhouse-based potted trial. For the field experiment, soils were categorized into three treatments based on *C. dendroides* coverage: high coverage (HCD), low coverage (LCD), and no coverage (NCD). Four forest microsites were considered: a gap in the mixed coniferous forest (GCF), a closed stand in the mixed coniferous forest (SCF), a gap in the mixed broadleaf–coniferous forest (GBC), and a closed stand in the mixed broadleaf–coniferous forest (SBC). The greenhouse experiment consisted of four treatments: HCD and LCD with similar *C. dendroides* coverage as the field experiment, litter-covered soil (LC), and bare soil (CK). *P. koraiensis* seeds were sown in each treatment's soil in both the field and greenhouse experiments and collected after one year to analyze their germination rates, decay rates, and antioxidant capacity based on each treatment. Correlations of the germination rate, decay rate, and antioxidant capacity of *P. koraiensis* seeds with the soil water content (SWC) and secondary metabolites of *C. dendroides* in soil were examined. The results revealed that, compared to soil without *C. dendroides*, HCD exhibited higher germination rates (increased by 15.2% and 32.5% for dormant field seeds and dormancy-broken greenhouse seeds, respectively), ABTS⁺ free radical scavenging activity (RSA_{ABTS}) (22.84% and 5.98% increases, respectively), catalase activity (CAT) (5.49 U·min^{−1}·g^{−1} and 1.71 U·min^{−1}·g^{−1} increases, respectively), and superoxide dismutase (SOD) activity (0.33 U·g^{−1} and 0.68 U·g^{−1} increases, respectively). In the field experiment, seeds in HCD exhibited higher DPPH free radical scavenging activity (RSA_{DPPH}) (26.24% increase) and peroxidase (POD) activity (4.0 U·min^{−1}·g^{−1} increase) compared to seeds in NCD. Greenhouse seeds in HCD showed a lower rot rate (27.6% decrease) than seeds in CK. In both the field and greenhouse experiments, SWC, soil p-hydroxybenzoic acid content (PHBA), soil p-coumaric acid content (PCMA), and soil vanillic acid content (VA) were significantly positively correlated with the germination rate and antioxidant capacity of *P. koraiensis*. Soil total phenolic content (TPH) and total flavonoid content (TFL) had minimal impacts on *P. koraiensis* seed germination. The primary findings suggest that *C. dendroides* may alleviate drought stress and enhance seed antioxidant and germination capabilities by increasing SWC, PHBA, PCMA, and VA.



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Keywords: seed germination; *Climacium dendroides*; *Pinus koraiensis*; soil water content; moss secondary metabolite

1. Introduction

Natural coniferous forests and mixed broadleaf Korean pine (*Pinus koraiensis*) forests represent two regional climax vegetation types in Northeast China [1]. The *P. koraiensis*

population has experienced a significant decline due to three catastrophic forestry events in the past century: the invasions of Tsarist Russia and Japan (1896–1945), the promotion of wood harvesting during forestry work (1950–1977), and the ‘Harvest quotas’ policy (1978–1998) [2]. *P. koraiensis* contributes to the improvement of soil physical and chemical properties, fertility, and carbon storage, similar to other tree species [3]. Additionally, it serves as a food source for various forest animals [4] and possesses economic value due to its edible kernels, medicinal needles, and quality timber [5]. Although the *P. koraiensis* population has partially recovered since the implementation of the Natural Forest Protection Project in 1998, its population density remains significantly lower than that of undisturbed natural forests [6]. In some stands, the mortality rate of red pine surpasses the renewal rate, resulting in a continued decline in population density [7]. Consequently, restoring the *P. koraiensis* population is crucial.

Climacium dendroides, a moss species distributed in Southwest and Northeast China, is an essential medicinal bryophyte resource [8]. Our preliminary observations have revealed many *P. koraiensis* seedlings in soil covered by *C. dendroides* (Figure 1), with none found in areas without *C. dendroides* coverage, suggesting a potential link between the environmental influence of *C. dendroides* and *P. koraiensis* regeneration. Mosses have been found to exert complex effects on the germination of vascular plants. Some studies have shown that mosses inhibit germination, such as in the case of *Typha latifolia*, where germination rates are significantly reduced in full moss carpets compared to bare peat [9]. Mosses may inhibit the germination of incoming seeds [10] and limit seed germination in semiarid and arid regions by reducing moisture [11,12] or by blocking light [13]. Conversely, mosses have been found to improve the germination of three desert plants in the Tengger Desert [14], and *Picea rubens* has been observed to prefer germinating and establishing on moss [15], as also seen in this study. Mosses facilitate *Picea mariana* germination by maintaining optimal environmental moisture and temperature [16]. The effect of moss on *Picea crassifolia* germination varies with moisture conditions, inhibiting germination when soil water content is high but promoting it when the soil is dry [17]. Therefore, moss plays an important role in the regeneration of vascular plants.



Figure 1. Natural regeneration of *P. koraiensis* in HCD (a) and LCD (b) soils.

Mosses may affect seed germination through several pathways. Firstly, they can regulate soil water content (SWC). Some studies have found that seeds experience lower rot rates under reduced SWC, which is beneficial for seed longevity [18,19]. In sandy areas, moss biocrust inhibits seed germination by decreasing SWC [12]. However, extremely high or low SWC negatively impacts seed germination [20,21]. Secondly, as a medicinal bryophyte, *C. dendroides* secretes numerous secondary metabolites [3], including phenolics and flavonoids [22,23], which exhibit significant inhibitory effects on plant pathogens [24,25]. These phenolics enhance plants' stress tolerance by increasing their antioxidant capacity [26–28], thereby reducing stress under adverse conditions [29]. This demonstrates that secondary metabolites from moss have been shown to enhance disease resistance and increase seed and plant survival rates.

Except for improving plant stress and disease resistance, numerous studies have reported that phenolics and flavonoids can promote seed germination and plant growth as biostimulants [30]. Plant-extract biostimulants have been found to stimulate seed germination and plant growth in a dose-dependent manner [31,32]. Low concentrations of plant extracts can promote seed germination, while high concentrations can inhibit germination [33]. Additionally, phenols can promote plant growth and development by regulating plant hormones, such as enhancing auxin, cytokinins, and gibberellins, and reducing abscisic acid levels [34]. Furthermore, they play a crucial role in improving plants' physiological characteristics [35]. Therefore, the regulation of *C. dendroides* on soil water content (SWC) and its secondary metabolite contents in the soil may play a significant role in *P. koraiensis* seed germination.

Based on the above information, we hypothesize that *C. dendroides* has a positive effect on *P. koraiensis* regeneration. To investigate the impact of *C. dendroides* on *P. koraiensis* regeneration, our study aimed to determine (1) whether *C. dendroides* improves *P. koraiensis* seed germination in both field and greenhouse experiments, (2) the extent to which *C. dendroides* affects *P. koraiensis* seed longevity by reducing seed rot rate, and (3) whether *C. dendroides* promotes *P. koraiensis* regeneration through secondary metabolites or changes in soil moisture content.

2. Materials and Methods

2.1. Research Site

The study area is located within the Liangshui National Nature Reserve (47°06' to 47°16' N, 128°47' to 128°57' E) in the Dailing District of Yichun City, Heilongjiang Province, People's Republic of China (P.R.C.) (Figure 2). The average annual temperature is −0.3 °C, with average annual maximum and minimum temperatures of −6.6 °C and 7.5 °C, respectively. The temperature can reach extremes as high as 38.7 °C and as low as −43.9 °C. The area receives an average annual precipitation of 676 mm, with 120–150 rainy days, primarily occurring between June and September. The average annual relative humidity is 78%, and the average annual evaporation is 805 mm. The region experiences approximately 1850 h of sunshine per year. The average annual ground temperature is 1.2 °C, with a frozen soil depth of about 2 m, and a frost-free period lasting between 100 and 120 days [36].

2.2. Field Experiment

2.2.1. Establishment of Sample Plots

In this study, two forest types (mixed coniferous forest and mixed broadleaved–coniferous forest) were chosen based on the abundance of *P. koraiensis* parent trees, seedling regeneration, and distribution of *C. dendroides*. The mixed coniferous forest primarily consisted of *Pinus koraiensis*, *Picea koraiensis*, and *Abies nephrolepis*, while the mixed broadleaved–coniferous forest was dominated by *Pinus koraiensis*, *Betula platyphylla*, *Picea koraiensis*, and *Acer mono*. A 100 m × 120 m sample plot was established in the mixed coniferous forest, and a 100 m × 100 m plot was established in the mixed broadleaved–coniferous forest, considering the area and topographic factors of the two forest types.

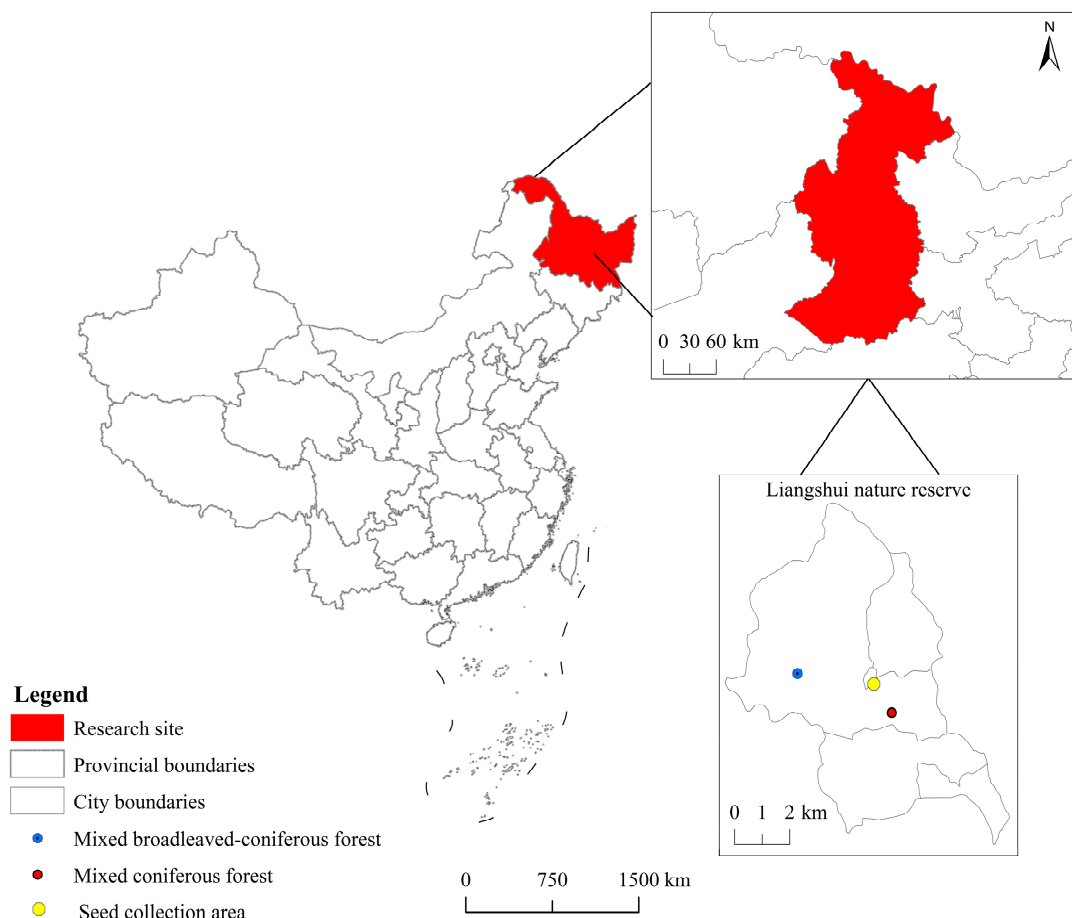


Figure 2. Location of the research site and seed collection area in the People's Republic of China.

2.2.2. Selection of Microsites and Experimental Design

As the selected forest types are natural forests, many gaps exist within the two plots due to the natural alteration of the forest canopies. Given that gaps can affect environmental conditions and subsequently influence *P. koraiensis* regeneration, gaps and stands were treated as distinct microsites. In the two sample plots, areas with $>4 \text{ m}^2$ openings in the forest canopy were classified as gaps, while other areas with intact forest canopy were considered closed stands. Thus, the two sample areas were divided into four forest microsites: the gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC).

Based on the extent of soil coverage by *C. dendroides*, the soil was divided into three treatments: HCD (high-coverage *C. dendroides*, $0.35\text{--}0.45 \text{ g}\cdot\text{cm}^{-2}$ (fresh mass of *C. dendroides*/soil area in October 2019) (Figure 1a)), LCD (low-coverage *C. dendroides*, $0.2\text{--}0.3 \text{ g}\cdot\text{cm}^{-2}$ (Figure 1b)), and NCD (no *C. dendroides* coverage, $0.0 \text{ g}\cdot\text{cm}^{-2}$). To estimate the fresh mass of *C. dendroides* and litter covering the soil surface (g/cm^2), 10 soil cover matter samples were randomly collected from each HCD and LCD treatment in each forest microsite using a $20 \text{ cm} \times 10 \text{ cm} \times 10 \text{ cm}$ (length $\times$ width $\times$ height) stainless steel frame (a total of 80 samples). Litter, *C. dendroides*, and other plants (live grass) were sorted, weighed, and calculated.

The calculation formula was as follows:

$$\text{Mass of litter and } C. \text{ dendroides} / \text{cm}^2 \text{ of soil surface} = \frac{\text{Mass of litter and } C. \text{ dendroides}}{\text{Length}(20 \text{ cm}) \times \text{width}(10 \text{ cm})}$$

Ten 10 cm × 10 cm quadrats were randomly placed within each treatment at various forest microsites, resulting in a total of 120 quadrats. *P. koraiensis* seeds exhibit dormancy [37], meaning that even when external conditions are conducive to germination, the seeds inhibit germination by employing physical barriers (such as air or water isolation), or by regulating their hormone and chemical levels [38]. In early October 2019, 80 dormant *P. koraiensis* seeds were sown in each quadrat. To protect the seeds from predation by rodents and birds, each quadrat was covered with a 10 cm × 10 cm metal mesh following seeding. Dormant seeds were utilized, because seeds with broken dormancy could not withstand the low winter temperatures. Under natural circumstances, *P. koraiensis* seeds break dormancy in specific early-spring environments [37]. For our field and greenhouse experiments, *P. koraiensis* seeds were collected from the Liangshui Nature Reserve in September 2019, with a 100-seed weight of 45.73 g (Figure 2).

2.2.3. Sample Collection

Topsoil samples (0–10 cm depth) were collected in June, August, and October 2020, at a distance of 5–15 cm from each quadrat. These samples were labeled based on the corresponding forest microsite and *C. dendroides* coverage within the quadrat. Upon returning to the laboratory, the soil samples were analyzed for soil water content (SWC), total phenolic content (TPH), total flavonoid content (TFL), and phenolic acid content.

2.3. Greenhouse Experiment

2.3.1. Treatment Design

Approximately 10 kg of soil was collected from an area 1 m away from the two sample plots of the field experiment. This soil was brought back to the laboratory, cleared of debris, thoroughly mixed, and used as the culture medium for the greenhouse experiment. Additionally, 5 kg of moss and litter from beneath the moss layer was collected and transported to the laboratory. Forty pots were filled with 700 g of soil each (top diameter: 15.5 cm; bottom diameter: 10.5 cm; height: 13.5 cm; soil filling height: approximately 9.5 cm; top surface diameter of the soil: about 14 cm).

The greenhouse experiment consisted of four treatments: CK, the control treatment with a bare soil surface and no cover; LC, where the soil surface was covered with 0.21 g·cm^{−2} of litter; LCD, which had 0.21 g·cm^{−2} of litter and 0.27 g·cm^{−2} of *C. dendroides* covering the soil surface; and HCD, which featured a soil surface covered with 0.21 g·cm^{−2} of litter and 0.4 g·cm^{−2} of *C. dendroides*. The mean litter mass per cm² in the LC, LCD, and HCD treatments was calculated based on the mean litter mass per cm² of all soil cover samples collected in the field. The *C. dendroides* mass per cm² in the LCD treatment was based on the *C. dendroides* mass per cm² in the LCD soil cover samples from the field experiments, while the *C. dendroides* mass per cm² in the HCD treatment was derived from the *C. dendroides* mass per cm² in the HCD soil cover samples from the field experiments.

2.3.2. Seed Pretreatments and Sample Collection

Considering the physiological dormancy habit of *P. koraiensis* seeds, we soaked them in a 50 µmol L^{−1} GA solution for 24 h prior to seeding to break dormancy [39]. In October 2019, 100 seeds were sown in each treated pot. To simulate rainfall conditions in the Liangshui area, 200 mL of water was added to each pot weekly (no watering occurred in January 2020, due to the impact of COVID-19). Watering ceased in October 2020, and the seeds in the pots were collected (some had germinated into seedlings) for the determination of germination and rot rates, as well as the antioxidant capacity of ungerminated seeds. Concurrently, soil samples from the pots were collected for the analysis of SWC, TPH, TFL, and phenolic acid content.

2.4. Identification and Calculation of the Germination Rate and Rot Rate of Seeds

The germination rate of *P. koraiensis* seeds was calculated by counting seeds with visible radicles emerging from the nutshells. For ungerminated seeds, the nutshells were opened,

and if the kernels were discolored or covered with mold, the seeds were considered rotten. All *P. koraiensis* seeds with ungerminated intact kernels were refrigerated for subsequent antioxidant capacity determination.

2.5. Determination of Soil and Seed Characteristics

Soil moisture content was measured using the oven-drying method. The total phenolic content in soil was determined by the Folin phenol method [40], and total flavonoid content was assessed using the aluminum nitrate–sodium nitrite colorimetric method [41]. Phenolic acids were analyzed by high-performance liquid chromatography (HPLC) using an Agilent 1260 Infinity II instrument (Germany). The chromatographic conditions were as follows: an Agilent ZORBAX SB-C18 column (5 μ m, 4.6 mm $\times$ 250 mm); column temperature, 35 $^{\circ}$ C; flow rate, 1.0 mL min⁻¹; mobile phase A, aqueous solution containing 0.1% formic acid; mobile phase B, methanol; gradient elution program [42]. Seed ABTS⁺ free radical scavenging activity (RSA_{ABTS}) and DPPH free radical scavenging activity (RSA_{DPPH}) were determined using spectrophotometry, following the method described by Xiang [43]. Superoxide dismutase (SOD) activity, peroxidase (POD) activity, and catalase (CAT) activity were determined using the nitrogen blue tetrazolium (NBT) colorimetric method, the guaiacol–hydrogen peroxide colorimetric method, and the ultraviolet absorption method, respectively [44]. A UV754N UV–visible spectrophotometer (Aplsh, China) was employed for these measurements.

2.6. Statistical Analysis

In the field experiments, the soil water content (SWC) and moss secondary metabolite levels in June, August, and October were averaged for each sample to obtain the mean value for each sample during the vegetation's growing season. Basic statistical analyses of the germination rate, rot rate, antioxidant capacity of seeds, SWC, and moss secondary metabolite contents in soil were conducted using SPSS 18. One-way ANOVA, followed by LSD tests, was employed to determine significant differences among the datasets. Bivariate correlation analysis was used to establish the correlation between seed germination rate, decay rate, antioxidant capacity, SWC, and moss secondary metabolite contents in the soil. Results were considered significant at $p < 0.05$. Bar charts were created using Origin 2021, while the R packages tidyverse and ggplot2 were utilized to generate correlation matrices.

3. Results

Within the same forest microsite, the germination rate of *P. koraiensis* seeds was significantly higher in HCD soil compared to LCD and NCD soils (11.55–18.92%, 6.46–9.90%, and 3.72–5.87%, respectively). In GCF and GBC, the germination rate of *P. koraiensis* seeds was significantly higher in LCD than in NCD, but there were no significant differences in SCF and SBC. In SCF, the rot rate of *P. koraiensis* seeds was significantly lower in NCD soil (5.25%) compared to other *C. dendroides* coverage soils (8.88% and 9.63%, respectively). Apart from SCF, *C. dendroides* coverage did not significantly affect the rot rate of *P. koraiensis* seeds in other microsites.

In all forest microsites, the DPPH free radical scavenging activity (RSA_{DPPH}) of *P. koraiensis* seeds was significantly higher in HCD soil than in NCD soil (46.77–49.62% and 23.38–35.43%, respectively). In GCF, there was no significant difference in the RSA_{DPPH} of *P. koraiensis* seeds between LCD and NCD soil; however, in other forest microsites, the RSA_{DPPH} of *P. koraiensis* seeds in LCD soil was significantly higher than that in NCD soil. In all forest microsites, the ABTS⁺ free radical scavenging activity (RSA_{ABTS}) of *P. koraiensis* seeds under different *C. dendroides* coverage levels was significantly different, with the order being HCD > LCD > NCD (49.00–52.05%, 39.22–44.11%, and 29.21–34.46%, respectively) (Figure 3).

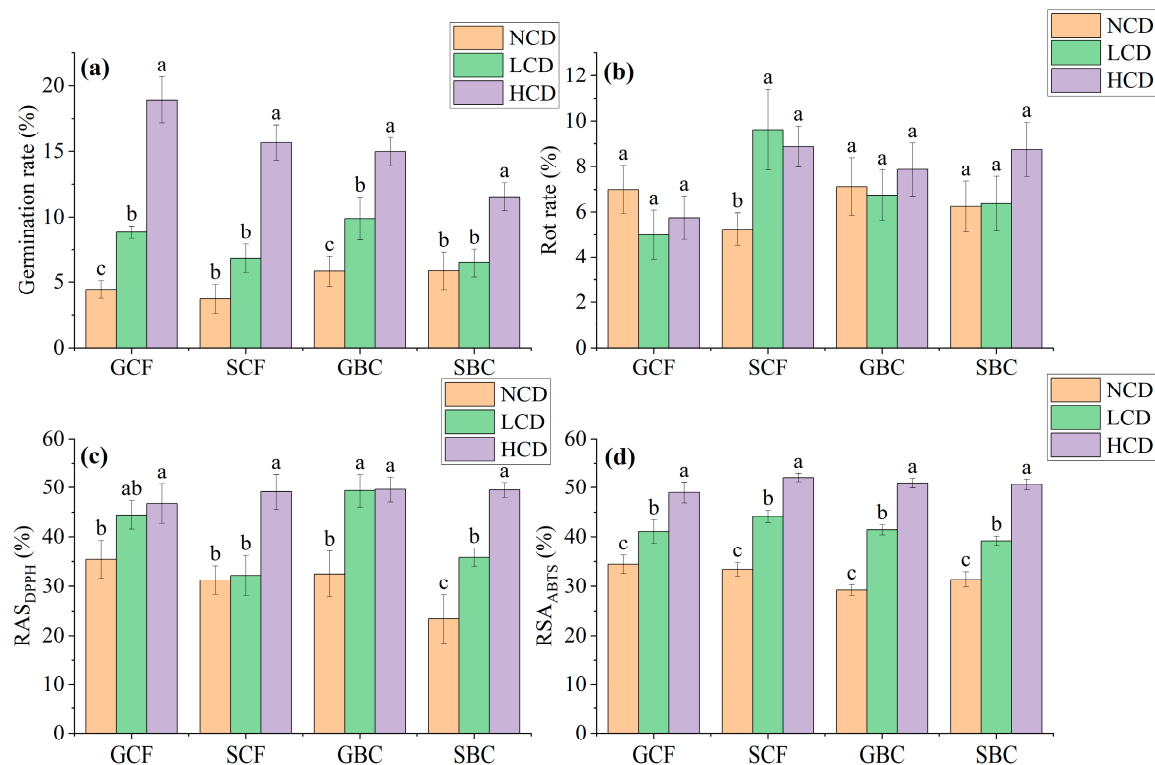


Figure 3. Differences in seed germination rate (a), rot rate (b), RSA_{DPPH} (c), and RSA_{ABTS} (d) among three *C. dendroides* coverages in four forest microsites. Different letters in columns show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

In all forest microsites, there were significant differences in the CAT activity of *P. koraiensis* seeds. Among the different *C. dendroides* coverage soils, the order of catalase (CAT) activity in *P. koraiensis* seeds was as follows: HCD > LCD > NCD ($6.60\text{--}7.09 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, $4.31\text{--}5.22 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, and $1.60\text{--}2.96 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, respectively). No significant differences in CAT activity were observed among the different forest microsites for HCD and LCD soils. In the GCF forest microsite, there were no significant differences in CAT activity for *P. koraiensis* seeds among different *C. dendroides* coverage soils. However, in other forest microsites, the peroxidase (POD) activity of *P. koraiensis* seeds in HCD soil was significantly higher than that in NCD soil ($8.10\text{--}8.80 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$ and $4.80\text{--}5.70 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, respectively). In SBC soil, no significant differences in the superoxide dismutase (SOD) activity of *P. koraiensis* seeds were observed, but in other forest microsites, the SOD activity of *P. koraiensis* seeds was significantly higher in HCD soil compared to NCD soil ($1.27\text{--}1.39 \text{ U} \cdot \text{g}^{-1}$ and $1.06\text{--}1.15 \text{ U} \cdot \text{g}^{-1}$, respectively) (Figure 4).

In the greenhouse experiments, *P. koraiensis* seeds exhibited a significantly higher germination rate and lower rot rate in *C. dendroides*-covered soil (LCD and HCD) compared to the CK and LC treatments (germination rate: 55.60%, 57.60%, 25.10%, and 32.20%, respectively; rot rate: 18.60%, 17.30%, 44.80%, and 41.10%, respectively). No significant differences were observed in RSA_{DPPH} for *P. koraiensis* seeds among the four treatments. The RSA_{ABTS} of *P. koraiensis* seeds was significantly higher in HCD soil compared to LC soil (48.68% and 42.70%, respectively), with no significant differences detected in the other treatments (Figure 5).

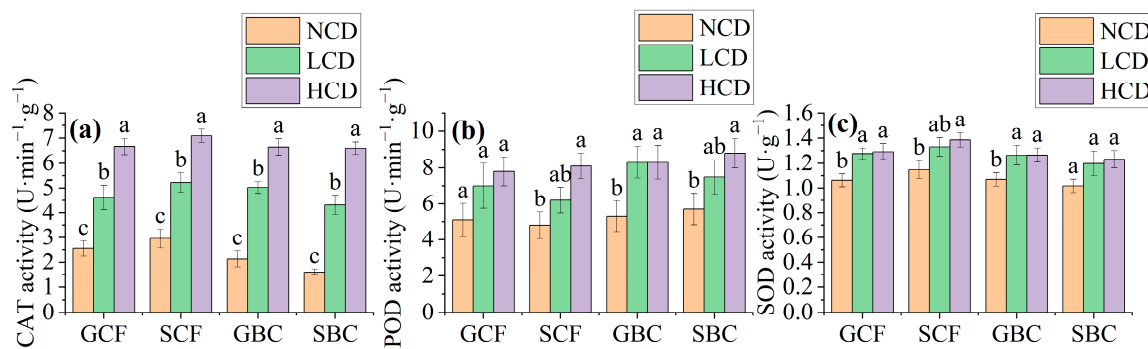


Figure 4. Differences in seeds' CAT activity (a), POD activity (b), and SOD activity (c) among three *C. dendroides* coverages in four forest microsites. Different letters in columns show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

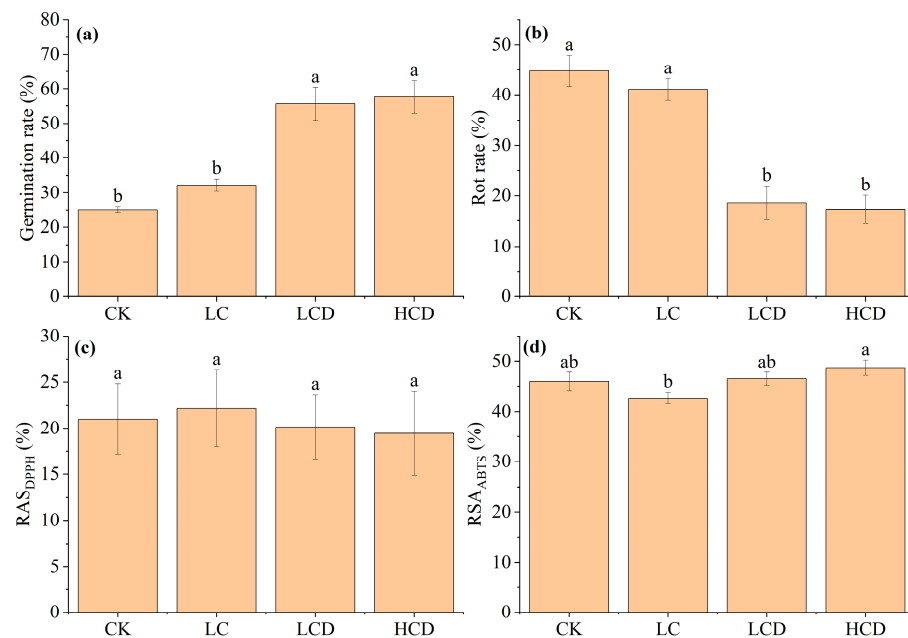


Figure 5. Differences in seeds' germination rate (a), rot rate (b), RSA_{DPPH} (c), and RSA_{ABTS} (d) among four treatments in the greenhouse experiments. Different letters in columns show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

In the greenhouse experiments, the CAT activity of *P. koraiensis* in the HCD treatment was significantly higher than that in bare soil ($4.87 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$ and $3.16 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, respectively), with no significant differences observed in the other treatments. The POD activity of *P. koraiensis* seeds showed no significant differences among the treatments. The SOD activity of *P. koraiensis* seeds in the LCD and HCD treatments was significantly higher than in bare soil ($2.14 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, $2.30 \text{ U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, and $\text{U} \cdot \text{min}^{-1} \cdot \text{g}^{-1}$, respectively), while the SOD activity of *P. koraiensis* seeds in the LC treatment did not differ significantly from the other three treatments (Figure 6).

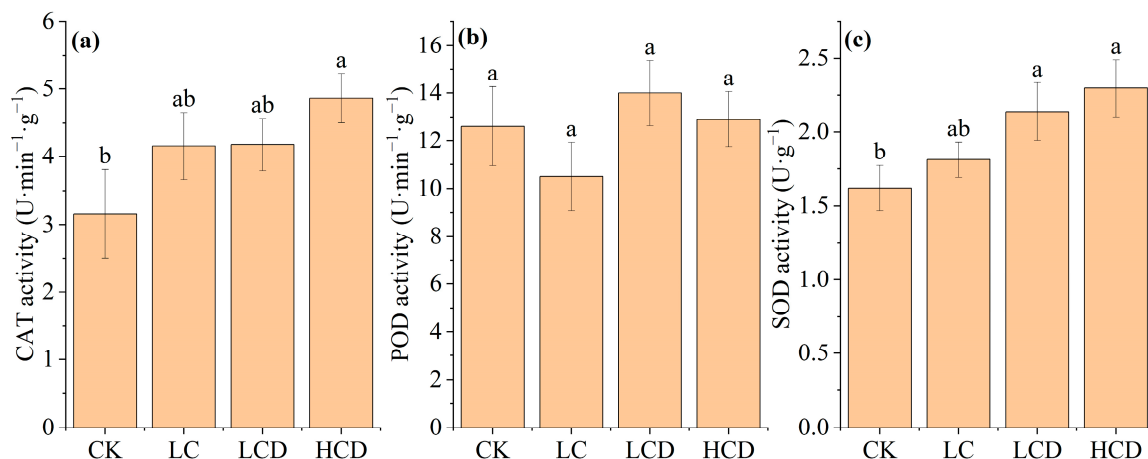


Figure 6. Differences in seeds' CAT activity (a), POD activity (b), and SOD activity (c) among four treatments in the greenhouse experiments. Different letters in columns show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

In the field experiments, in all forest microsites, the soil water content (SWC) showed significant differences among soils with different *C. dendroides* coverage; the order of SWC in the three soils by *C. dendroides* coverage was HCD > LCD > NCD. In all forest microsites, the soil TPH contents showed no significant differences among the three soils. In the MCG, MCS, and BCS forest microsites, the soil TFL contents were significantly higher in HCD soil than in LCD soil. In the MCG forest microsite, the soil TFL contents were significantly higher in HCD soil than in NCD. In MCS and BCS, the soil TFL contents showed no significant differences between HCD and NCD soil. In BCG, the soil TFL contents had no significant differences in the three soils. In the MCS forest microsite, there were no significant differences in the soil SA contents in the three soils with different *C. dendroides* coverage. In the other three forest microsites, the soil SA contents were significantly higher in NCD soil than in LCD and HCD soil. In the MCG and BCG forest microsites, LCD soil had higher SA contents than HCD soil. In all four forest microsites, the soil PHBA contents were significantly different among the three *C. dendroides* coverage soils; the order of soil PHBA contents in the three soils was HCD > LCD > NCD. In the MCG and MCS forest microsites, the soil PCMA contents were significantly higher in LCD and HCD soils than in NCD soil. However, in the BCG and BCS forest microsites, the order of soil PCMA contents in the three soils by *C. dendroides* coverage was HCD > LCD > NCD. In all four forest microsites, the soil VA contents were significantly higher in LCD and HCD soils than in NCD soil (Table 1).

In the greenhouse experiments, the soil water content (SWC) was significantly higher in the HCD and LCD treatments compared to the LC and CK treatments. The soil total phenolic content (TPH), total flavonoid content (TFL), and SA content showed no significant differences among the treatments. The soil PHBA contents in the different treatments followed the order HCD > LCD > LC and CK. The soil PCMA content was higher in HCD compared to the other three treatments (LCD, LC, and CK). The soil VA content was significantly higher in HCD and LCD soils than in LC and CK (Table 2).

Table 1. Soil water content and moss secondary metabolite contents in soils with different *C. dendroides* coverage in the field experiments.

Forest Microsites	Treatments	SWC (%)	TPH (mg/g)	TFL (mg/g)	SA (µg/g)	PHBA (µg/g)	PCMA (µg/g)	VA (µg/g)
GCF	NCD	39.05 (0.55) c	1.22 (0.08) a	2.40 (0.31) b	0.58 (0.02) a	0.72 (0.02) c	1.08 (0.03) b	0.70 (0.03) b
	LCD	45.49 (0.55) b	1.02 (0.55) a	2.21 (0.55) b	0.46 (0.55) b	0.99 (0.55) b	1.90 (0.55) a	1.15 (0.55) a
	HCD	50.87 (0.39) a	1.40 (0.28) a	3.65 (0.64) a	0.35 (0.01) c	1.35 (0.09) a	1.85 (0.18) a	1.13 (0.08) a
SCF	NCD	32.56 (0.22) c	1.24 (0.12) a	4.10 (0.20) ab	0.54 (0.07) a	0.71 (0.08) c	0.98 (0.13) b	0.71 (0.08) b
	LCD	39.56 (0.25) b	1.27 (0.11) a	2.41 (0.16) b	0.40 (0.02) a	0.92 (0.04) b	1.77 (0.11) a	1.08 (0.08) a
	HCD	43.46 (0.35) a	1.36 (0.18) a	5.53 (1.01) a	0.45 (0.06) a	1.24 (0.05) a	1.81 (0.07) a	1.25 (0.09) a
GBC	NCD	36.28 (0.24) c	1.35 (0.12) a	1.95 (0.13) a	0.53 (0.02) a	0.67 (0.04) c	1.09 (0.02) c	0.76 (0.04) b
	LCD	39.54 (0.32) b	1.12 (0.12) a	1.49 (0.07) a	0.44 (0.01) b	1.00 (0.01) b	1.61 (0.07) b	1.19 (0.04) a
	HCD	42.70 (0.30) a	1.21 (0.12) a	2.21 (0.57) a	0.38 (0.01) c	1.35 (0.02) a	2.09 (0.06) a	1.13 (0.04) a
SBC	NCD	27.11 (0.45) c	1.37 (0.16) a	3.01 (0.18) a	0.53 (0.02) a	0.80 (0.05) c	1.06 (0.06) c	0.97 (0.08) b
	LCD	30.71 (0.30) b	1.26 (0.14) a	1.66 (0.04) b	0.43 (0.01) b	0.96 (0.07) b	1.73 (0.13) b	1.48 (0.10) a
	HCD	36.10 (0.34) a	1.16 (0.15) a	3.74 (0.71) a	0.37 (0.03) b	1.12 (0.03) a	2.30 (0.09) a	1.34 (0.04) a

Values in parentheses are standard errors. Different letters in columns for each microsite show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

Table 2. Soil water content and moss secondary metabolite contents in different soil treatments in the greenhouse experiments.

Treatments	SWC (%)	TPH (mg/g)	TFL (mg/g)	SA (µg/g)	PHBA (µg/g)	PCMA (µg/g)	VA (µg/g)
CK	5.73 (0.34) b	0.30 (0.01) a	1.73 (0.16) a	0.36 (0.02) a	0.50 (0.03) c	1.08 (0.08) b	0.68 (0.08) b
LC	7.98 (0.57) b	0.31 (0.01) a	1.72 (0.14) a	0.37 (0.01) a	0.55 (0.05) c	1.19 (0.17) b	0.83 (0.11) b
LCD	23.96 (1.35) a	0.30 (0.02) a	1.36 (0.15) a	0.40 (0.04) a	0.69 (0.05) b	1.39 (0.14) b	1.44 (0.03) a
HCD	24.80 (1.87) a	0.32 (0.01) a	1.79 (0.18) a	0.42 (0.03) a	0.82 (0.05) a	2.13 (0.08) a	1.44 (0.06) a

Values in parentheses are standard errors. Different letters in columns show significant differences as determined by the LSD method ($p < 0.05$). The gap in the mixed coniferous forest (GCF), the closed stand in the mixed coniferous forest (SCF), the gap in the mixed broadleaf–coniferous forest (GBC), and the closed stand in the mixed broadleaf–coniferous forest (SBC); high-coverage *C. dendroides* (HCD), low-coverage *C. dendroides* (LCD), and no *C. dendroides* (NCD).

In the field experiments, the soil water content (SWC), PHBA, and VA contents were significantly and positively correlated with the *P. koraiensis* seed germination rate ($r = 0.586$, $p < 0.05$; $r = 0.558$, $p < 0.05$; $r = 0.273$, $p < 0.05$, respectively), RSA_{DPPH} ($r = 0.439$, $p < 0.05$; $r = 0.440$, $p < 0.05$; $r = 0.310$, $p < 0.05$, respectively), RSA_{ABTS} ($r = 0.520$, $p < 0.05$; $r = 0.693$, $p < 0.05$; $r = 0.501$, $p < 0.05$, respectively), CAT ($r = 0.584$, $p < 0.05$; $r = 0.704$, $p < 0.05$;

$r = 0.422$, $p < 0.05$, respectively), POD ($r = 0.191$, $p < 0.05$; $r = 0.334$, $p < 0.05$; $r = 0.339$, $p < 0.05$, respectively), and SOD activity ($r = 0.304$, $p < 0.05$; $r = 0.395$, $p < 0.05$; $r = 0.250$, $p < 0.05$, respectively). Soil total phenolic content (TPH) showed no significant correlation with *P. koraiensis* seed germination rate, rot rate, or antioxidant capacity. Soil flavonoid content (TFL) was positively correlated with *P. koraiensis* seed RSA_{ABTS} and CAT activity. Soil SA content was significantly and negatively correlated with *P. koraiensis* seed germination rate, RSA_{DPPH}, RSA_{ABTS}, CAT, and POD activity ($r = -0.426$, $p < 0.05$; $r = -0.211$, $p < 0.05$; $r = -0.448$, $p < 0.05$; $r = -0.449$, $p < 0.05$; $r = -0.243$, $p < 0.05$, respectively). Soil PCMA content was significantly and positively correlated with *P. koraiensis* seed germination rate, rot rate, RSA_{DPPH}, RSA_{ABTS}, CAT, POD, and SOD activity ($r = 0.486$, $p < 0.05$; $r = 0.190$, $p < 0.05$; $r = 0.435$, $p < 0.05$; $r = 0.652$, $p < 0.05$; $r = 0.684$, $p < 0.05$; $r = 0.361$, $p < 0.05$; $r = 0.229$, $p < 0.05$, respectively) (Figure 7). These results suggest that *C. dendroides* can promote seed germination and enhance the antioxidant capacity of seeds by regulating SWC, PHBA, PCMA, and VA.

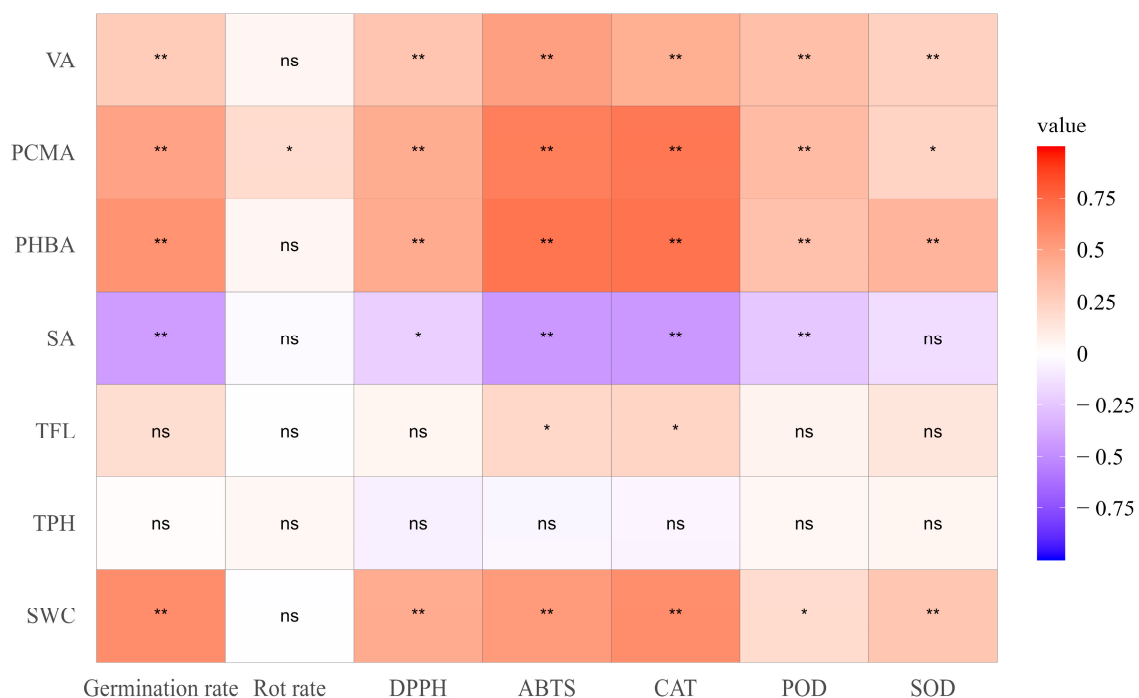


Figure 7. Pearson's correlation coefficients (r) between *P. koraiensis* seeds' germination characteristics and soil water content and moss secondary metabolite contents in the field experiments; * significant at $p < 0.05$, ** significant at $p < 0.01$, ns: no significant correlation between these factors.

In the greenhouse experiments, the soil water content (SWC), soil PHBA, and VA contents were significantly and positively correlated with the *P. koraiensis* seed germination rate ($r = 0.850$, $p < 0.05$; $r = 0.523$, $p < 0.05$; $r = 0.802$, $p < 0.05$, respectively), RSA_{ABTS} ($r = 0.338$, $p < 0.05$; $r = 0.454$, $p < 0.05$; $r = 0.368$, $p < 0.05$, respectively), and SOD activity ($r = 0.453$, $p < 0.05$; $r = 0.361$, $p < 0.05$; $r = 0.405$, $p < 0.05$, respectively), while being negatively correlated with the *P. koraiensis* seed rot rate. Soil TPH content demonstrated a negative correlation with *P. koraiensis* seed RSA_{DPPH} ($r = -0.419$, $p < 0.05$). Soil TFL content showed no significant correlation with any *P. koraiensis* seed germination characteristics. Soil SA content was significantly and positively correlated with *P. koraiensis* seed germination rate and RSA_{DPPH}, while being negatively correlated with the seed rot rate ($r = 0.460$, $p < 0.05$; $r = 0.457$, $p < 0.05$; $r = -0.501$, $p < 0.05$, respectively). Soil PCMA content was positively correlated with the *P. koraiensis* seed germination rate but negatively correlated with the seed rot rate ($r = 0.478$, $p < 0.05$; $r = -0.479$, $p < 0.05$, respectively) (Figure 8). These findings indicate that, in the greenhouse experiments, SWC, SA, PHBA, and VA contributed to enhancing the seed germination rate and antioxidant capacity while preventing seed rot.

Additionally, PCMA improves the germination rate and reduces the rot rate but does not affect the antioxidant capacity of seeds.

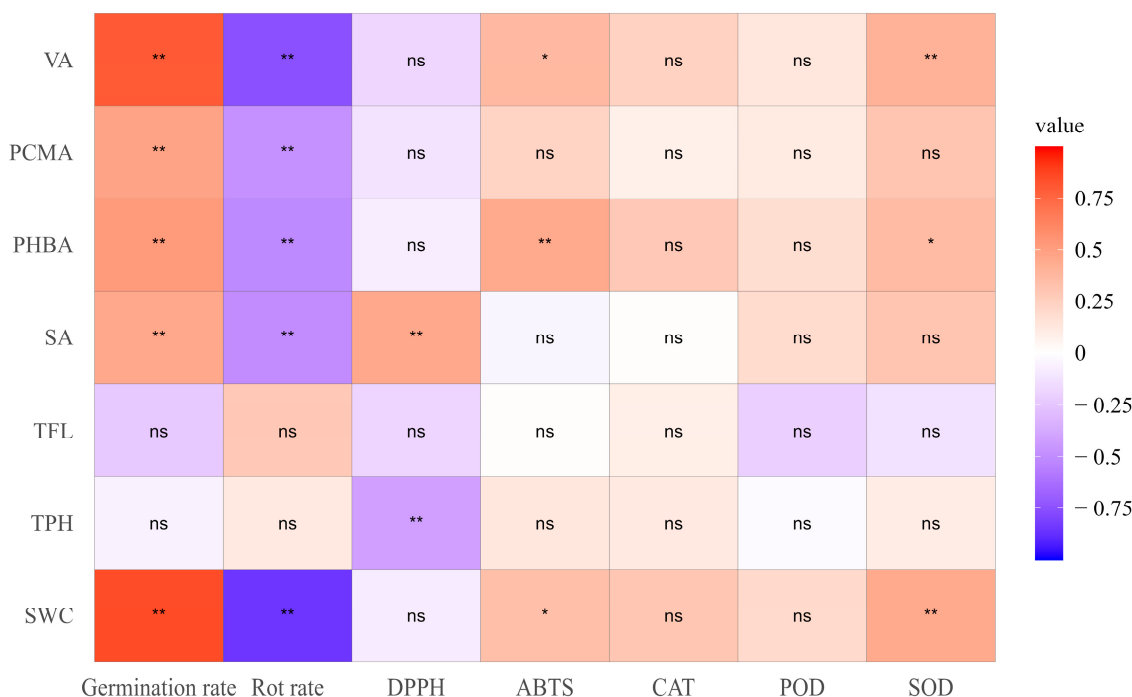


Figure 8. Pearson's correlation coefficients (r) between *P. koraiensis* seeds germination characteristics and soil water content and moss secondary metabolite contents in the greenhouse experiments; * significant at $p < 0.05$, ** significant at $p < 0.01$, ns: no significant correlation between these factors.

4. Discussion

4.1. Germination Ability of *P. koraiensis* in Soils with Different *C. dendroides* Coverage

Moss cover has been found to facilitate the establishment of vascular plants in Mediterranean steppes [45]. Our study showed that *P. koraiensis* seeds had a higher germination rate in *C. dendroides*-covered soils (HCD and LCD) compared to NCD soil. However, there were no differences in the seed rot rate among the three soils with different *C. dendroides* coverage in the field experiments. This demonstrates that moss may improve regeneration by promoting dormant seed germination without inhibiting seed rot; in fact, moss even increased the seed rot rate in the SCF microsite. In contrast, in the greenhouse experiments, dormancy-broken seeds exhibited a higher germination rate and lower rot rate in HCD and LCD soils compared to LC and CK. This result indicates that moss enhances germination and inhibits rot in dormancy-broken seeds, which exhibited both higher germination rates and higher rot rates than dormant seeds. Our findings are consistent with other studies [14–16], suggesting that *C. dendroides* provides a more favorable water environment for seed germination, unlike other mosses [10–12] that compete with vascular plants for water and inhibit germination.

Regarding the shading effect of moss [13], red pine is shade-tolerant at the seedling stage, so the phenomenon of moss shading inhibiting plant regeneration did not appear in this study. In our research, moss was able to not only promote seed germination but also release seed dormancy. Thus, in field experiments, there may be more dormancy-broken seeds in *C. dendroides*-covered soils, which can improve seed germination rates. However, seed dormancy effectively prevents seed rot [46], so the seed rot rate did not decrease significantly in *C. dendroides*-covered soils but instead increased the rot rate in the SCF microsite. In the greenhouse experiments, where all seeds were dormancy-broken, moss decreased rather than increased the seed rot rates. Seeds produce reactive oxygen species during germination or under stress conditions, potentially causing cellular damage,

germination inhibition, and seed death [47]. Therefore, enhancing seeds' antioxidant potential favors seed germination and survival [48]. In our field experiments, seeds in HCD soil exhibited higher RSA_{DPPH} , POD, and SOD activities than those in NCD soil. The seed RSA_{ABTS} and CAT activities in the three *C. dendroides*-covered soils followed the order $\text{HCD} > \text{LCD} > \text{NCD}$. In our greenhouse experiments, HCD soil improved seeds' antioxidant potential by increasing their RSA_{ABTS} , CAT, and SOD activities, while LCD soil enhanced the seeds' SOD activity. This suggests that *C. dendroides*-covered soils improve seeds' germination and survival by augmenting their antioxidant potential.

4.2. *C. dendroides* Influences *P. koraiensis* Germination Ability by Modulating SWC and Secondary Metabolites in Soil

Optimal moisture conditions are necessary for seed germination [21], and deviations from optimal moisture levels can inhibit seed germination [49]. In our study, we observed that soil water content (SWC) increased with *C. dendroides* coverage, which was accompanied by an increase in the seed germination rate. Our analysis revealed no significant effect of soil water content on seed rot; however, soil water content was significantly and positively correlated with seed germination and antioxidant potential. This suggests that the SWC in NCD soil is below optimal levels, subjecting seeds to drought stress. *C. dendroides* enhances seed germination by improving the soil water content and reducing drought stress.

Exogenous flavonoids have been shown to significantly improve seed stress resistance [50], and they can promote seed germination, particularly under stress conditions [51]. In our field experiments, HCD soil exhibited the highest total flavonoid (TFL) content, while LCD soil had lower TFL content. Soil TFL was not correlated with germination or rot rates but was positively correlated with RSA_{ABTS} and CAT activity. However, in the greenhouse experiments, no significant differences in soil TFL were observed between treatments, and no significant correlation was found between *P. koraiensis* seed germination characteristics. The effect of *C. dendroides* on soil TFL may result from long-term accumulation, leading to significant differences in field experiments but not in greenhouse settings. Nevertheless, soil TFL only improves seed stress resistance by increasing antioxidant capacity, without promoting seed germination.

Phenolic compounds exhibit complex effects on seed germination, with different impacts on various plants [52]. Generally, low concentrations of phenolic substances can promote seed germination, while high concentrations of phenolic acids can inhibit germination [33]. Numerous phenolic acids at high concentrations (above 20 mM)—including syringic acid, p-coumaric acid, p-hydroxybenzoic acid, and vanillic acid—have been reported to inhibit seed germination [52]. In both field and greenhouse experiments, *C. dendroides* coverage did not significantly affect soil total phenolic (TPH) contents, and from a correlation standpoint, soil TPH did not promote *P. koraiensis* seed germination. This indicates that *C. dendroides* does not promote seed germination by altering soil TPH.

In field and greenhouse experiments, as *C. dendroides* coverage increased, soil p-hydroxybenzoic acid (PHBA), p-coumaric acid (PCMA), and vanillic acid (VA) concentrations also increased to varying extents, while syringic acid (SA) concentrations did not increase significantly or even decreased in the field experiments. Soil PHBA, PCMA, and VA in the field experiments and all four phenolic acids in the greenhouse experiments were positively correlated with either the seed germination rate or both the germination rate and antioxidant capacity. This phenomenon may be attributed to exogenous phenols promoting seed germination [53] by stimulating the pentose phosphate pathway and antioxidant enzyme system [54], as seen in Peng's study, where caffeic acid significantly increased the seeds' germination rate and antioxidant capacity [55]. In the field experiments, soil PCMA was found to be significantly and positively correlated with the rot rate of dormant seeds. In contrast, in greenhouse conditions, the concentrations of four phenolic acids in the soil exhibited a significant negative correlation with the rot rate of dormancy-broken seeds. Phenolic acids have been shown to have a notable inhibitory effect on plant pathogens [24],

and to enhance plant stress resistance [56]. This could explain the observed negative correlation between the four phenolic acids and the rot rate of dormancy-broken seeds.

Soil PCMA's significant positive correlation with the rot rate of dormant seeds could be attributed to the fact that the rot is inhibited by the dormancy habit of *P. koraiensis* itself [37,46,57]. Soil PCMA, like other phenolic acids such as salicylic acid [58], can alleviate seed dormancy, causing seeds to lose the protection provided by dormancy and, subsequently, increasing the rot rate. However, this does not necessarily imply that the seed mortality rate will increase. Rather, ungerminated seeds will not have the opportunity to emerge from dormancy until the following spring, approximately 20 months after being planted. During this period, they face a high likelihood of being consumed by forest rodents and insects, with most ungerminated seeds not surviving until the next spring [59]. In other words, the seeds will either be released from dormancy to decay or germinate, or they will be consumed by predators.

5. Conclusions

C. dendroides was beneficial to the regeneration of *P. koraiensis* by improving the germination rate and antioxidant capacity of dormant and dormancy-broken *P. koraiensis* seeds, while decreasing the rot rate of dormancy-broken seeds. The reason for this phenomenon may be that *C. dendroides* can effectively increase soil's water content and phenolic acid content, which is conducive to seed germination, and phenolic acid is beneficial for the inhibition of pathogens, improving the antioxidant capacity of seeds, improving seed stress resistance, and other comprehensive results.

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