Ecophysiological responses of fine roots of Chinese fir seedlings and associated plants to soil warming: Postprint

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Abstract

To reveal the competitive relationships and adaptability for soil nutrients between Chinese fir (Cunninghamia lanceolata) plantation seedlings and their associated plants under global warming, this study employed soil warming (+5°C) technology via buried heating cables to establish experimental plots of Chinese fir seedlings at Chenda State-owned Forest Farm in Sanming City, Fujian Province, including control (NW) and warming (WNW) treatments (both without weeding). Using a combination of the ingrowth core method and soil coring method, the short-term effects of warming on fine root biomass, respiration, morphology, and root tissue nitrogen concentration of Chinese fir seedlings and associated plants (mainly Helicteres angustifolia and Mallotus lianus) were measured. The results showed that: (1) Warming significantly reduced the <1 mm fine root biomass of Chinese fir, while significantly increasing the <1 mm fine root biomass of other plants. Warming significantly increased the nitrogen concentration of <1 mm fine roots of other plants, significantly decreased their specific root length (SRL) and specific surface area (SRA), and concurrently reduced specific root respiration (reference temperature 18°C, SRR18), indicating that fine root respiration exhibited acclimation to warming. In contrast, warming had no significant effect on the nitrogen concentration of Chinese fir fine roots, but significantly increased the specific surface area of <1 mm fine roots; meanwhile, warming had no significant effect on SRR18 of Chinese fir, indicating that Chinese fir fine root respiration did not exhibit acclimation. (2) The relationship between SRR18u and specific root length was significantly affected by warming, but tree species and the warming × species interaction had no significant effects, indicating that the balance between competitive ability and maintenance cost of fine roots in both Chinese fir and other plants was jointly influenced by warming. In summary, the results demonstrate that compared with Chinese fir, the associated other plants possess stronger competitive advantages for belowground resources in a warming environment, capable of rapidly seizing and absorbing soil nutrients whose mineralization is accelerated by warming through increased fine root biomass, while simultaneously reducing maintenance cost per unit root mass through physiological and morphological adjustments, thereby enhancing their adaptability to global warming; whereas Chinese fir faces intense competition from other plants under warming conditions, with reduced fine root biomass and a disadvantaged position; to meet growth requirements, it needs to increase specific root length and specific root surface area, and due to the lack of acclimation in fine root respiration, this increases the maintenance cost per unit fine root mass, indicating that Chinese fir has lower adaptability to global warming than other plants. These research findings hold significant implications for the management of Chinese fir plantations under global warming.

Full Text

Preamble

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The Ecophysiological Responses of Fine Roots of Chinese Fir (*Cunninghamia lanceolata*) Seedlings and Associated Plants to Soil Warming

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Abstract

To reveal the competitive relationships and adaptive strategies for soil nutrients between Chinese fir (*Cunninghamia lanceolata*) plantation seedlings and associated plants under global warming, we conducted a soil warming experiment using buried heating cables at Chenda State-Owned Forest Farm in Sanming City, Fujian Province. The study established three non-weeding control (NW) and three non-weeding warming (WNW) 2 m × 2 m plots with Chinese fir seedlings and naturally occurring associated plants (*Helicteres angustifolia*, *Mallotus lianus*, etc.). Fine root biomass was measured using a combination of soil coring and ingrowth core methods. Specific root respiration rates were measured with a Clark-type oxygen electrode, root morphology was analyzed with WinRHIZO Pro 2009b software, and root tissue nitrogen concentration was determined using a vario EL III Element Analyzer.

The results showed that: (1) Soil warming significantly decreased the fine root biomass (<1 mm) of Chinese fir while significantly increasing that of associated plants. Warming significantly increased root tissue nitrogen concentration and specific root area (SRA) of associated plants, but decreased their specific root length (SRL) and specific root respiration rate measured at a reference temperature of 18°C (SRR), indicating that root respiration showed acclimation to warming. For Chinese fir seedlings, warming had no significant effect on SRR or root tissue nitrogen concentration, except that SRA of <1 mm roots significantly increased. (2) Soil warming significantly influenced the relationship between SRR and SRL; however, tree species and the warming × species interaction had no significant effect, indicating that the balance between root absorptive capacity and maintenance cost was affected by warming in both Chinese fir and associated plants.

In conclusion, compared with Chinese fir seedlings, associated plants exhibited stronger competitive advantages for belowground resources and higher adaptability to soil warming. They rapidly captured mineralized soil nutrients accelerated by warming through increased fine root biomass, while simultaneously reducing per-unit-mass maintenance costs through physiological and morphological adjustments (including respiration acclimation). Chinese fir, however, faced intense competition from other plants under warming conditions. To meet growth requirements despite reduced fine root biomass, Chinese fir had to increase SRL and SRA, but without respiration acclimation, leading to increased per-unit-mass maintenance costs. This suggests that Chinese fir has lower adaptability to global warming than associated plants. These findings have important implications for managing Chinese fir plantations under global warming scenarios, particularly regarding the need for effective weed control measures.

Keywords: warming; competition; adaptability; specific root respiration; fine root morphology; root tissue nitrogen concentration; acclimation

1. Study Site and Warming Experiment

The warming experiment was conducted at Chenda State-Owned Forest Farm in Jinsiwan Forest Park, Sanming City, Fujian Province (26°19 N, 117°36 E). The region has a mid-subtropical monsoon climate with a mean annual temperature of 19.1°C and mean annual precipitation of 1,749 mm. The experiment employed a completely randomized design with two treatments: non-weeding control (NW) and non-weeding warming (WNW), each with three replicates.

Experimental plots (2 m × 2 m) were established on an open, flat area. Each plot was isolated from surrounding soil, and filled with soil collected from a nearby Chinese fir forest. After removing stones and debris, the soil was mixed by layer (0–10, 10–20, and 20–70 cm) and backfilled according to original layer order.

Soil bulk density was adjusted using a compaction method to match natural conditions (Table 1). In March 2014, heating cables were buried at 20 cm depth in a grid pattern, with an additional loop around the perimeter to ensure uniform warming. Control plots contained non-functional cables. Each plot was planted with 18 half-sib Chinese fir seedlings positioned between cable lines. Naturally germinated plants were retained to observe competition dynamics, including *Helicteres angustifolia*, *Mallotus lianus*, *Rhus chinensis*, and *Scleria elata*.

The warming system maintained soil temperature at 5 ± 0.5°C above ambient background temperature. To examine fine roots of similar age, ingrowth cores (20 cm diameter × 20 cm depth) were installed at each plot center in March 2015. During installation, the core was driven into the soil, then soil was excavated from inside, all roots were removed, and the original soil was backfilled, allowing new root growth for analysis.

** Table 1 Soil bulk density prior to and after backfilling at different depths**

** Table 2 Soil ammonium and nitrate nitrogen content in control (NW) and warming (WNW) plots**

[Figure 1: see original paper] Fig. 1 Soil temperature and moisture content in control (NW) and warming (WNW) treatments from March 2014 to July 2015

** Table 3 Tree number (strain/m²), mean ground diameter (mm), and mean height (cm) of Chinese fir seedlings and associated plants**

** Table 4 Aboveground biomass, underground biomass, and total biomass of Chinese fir seedlings and associated plants (g/m²)**

2. Fine Root Biomass Measurement

Fine roots were sampled using soil cores (3.5 cm diameter) to a depth of 60 cm. Sampling points were randomly distributed across each plot, avoiding cable locations and ensuring representation of both center and edge areas. Live roots were identified by color, elasticity, and morphology. Chinese fir roots were distinguished by their characteristics: new fine roots were plump with white epidermis, older roots turned reddish-white or dark red, and lignified roots had peeled epidermis with dark red inner bark. Remaining roots were classified as other plants.

Roots were separated into two diameter classes: 0–1 mm (absorptive roots) and 1–2 mm (structural roots), based on preliminary observations that most absorptive roots of Chinese fir and associated plants fell within the <1 mm range. After cleaning, roots were oven-dried at 65°C and weighed. Fine root biomass (g/m²) was calculated based on sample area.

3. Fine Root Physiological and Ecological Characteristics Measurement

Soil from ingrowth cores (0–20 cm depth) was excavated and brought to the laboratory. All roots were extracted, washed, and separated into Chinese fir and other plant roots, then divided into 0–1 mm and 1–2 mm diameter classes. This ingrowth core method ensured that measured roots were newly produced after warming treatment with similar age, better reflecting warming effects on root ecophysiological characteristics.

For respiration measurements, subsamples from each diameter class were placed in physiological buffer solution (10 mmol/L MES, 1 mmol/L CaSO) at 18°C for 10 minutes to equilibrate, then measured using a Clark-type oxygen electrode (Oxytherm). Each diameter class from each plot was measured once to minimize error. After measurement, roots were scanned at 300 dpi using an Epson scanner, and root architecture and morphology (length, surface area) were analyzed with WinRHIZO Pro 2009b software. Roots were then oven-dried at 65°C for dry weight measurement.

Specific root length (SRL, m/g) was calculated as root length divided by dry weight. Specific root area (SRA, cm^2/g) was calculated as root surface area divided by dry weight. Specific root respiration rate (SRR , nmol O g^{1} s^{1}) was calculated based on root dry weight at the reference temperature of 18°C. Root tissue nitrogen concentration was determined using a vario EL III Element Analyzer after grinding dried samples with a ball mill.

4. Data Analysis

SPSS 19.0 software was used for statistical analyses. One-way ANOVA compared fine root biomass, SRL, SRA, and SRR among treatments and species. Multi-factor ANOVA examined effects of warming, species, and diameter class on root tissue nitrogen concentration. Because SRR and SRL follow a power function relationship, natural logarithms were taken and linear regression was performed. Covariance analysis tested effects of warming and species on the SRR -SRL relationship.

1. Effects of Warming on Fine Root Biomass

Warming treatment significantly affected fine root biomass ($P < 0.001$), as did the interaction between species and diameter class ($P < 0.001$). Chinese fir and associated plants showed significantly different fine root biomass ($P < 0.001$). For 0–1 mm roots, biomass was (27.92 ± 2.08) g/m^2 for Chinese fir and (86.60 ± 37.51) g/m^2 for associated plants in control plots, versus (24.44 ± 8.27) g/m^2 and (423.58 ± 124.18) g/m^2 in warmed plots, respectively. For 1–2 mm roots, values were (54.31 ± 30.42) g/m^2 and (27.12 ± 14.79) g/m^2 in control plots, versus (63.72 ± 16.33) g/m^2 and (290.69 ± 73.56) g/m^2 in warmed plots.

Warming significantly decreased Chinese fir fine root biomass ($P < 0.01$) while significantly increasing that of associated plants ($P < 0.01$). However, warming had no significant effect on 1-2 mm root biomass for either Chinese fir or associated plants ($P > 0.05$).

[Figure 2: see original paper] Fig. 2 Fine root biomass by treatments and species for 0-1 mm and 1-2 mm diameter classes

** Table 5 Analysis of variance for the effects of soil warming on root biomass, specific root respiration rate, specific root length, specific root area, and tissue N concentration for Chinese fir seedlings and associated plants**

2. Effects of Warming on Root Tissue Nitrogen Concentration

Warming treatment, species, and their interaction had no significant effect on root tissue nitrogen concentration ($P > 0.05$), but diameter class had a highly significant effect ($P < 0.001$), as did the interaction between species and diameter class ($P < 0.05$). For 0–1 mm roots, tissue nitrogen concentrations were (10.87 ± 1.35) mg/g for Chinese fir and (11.78 ± 1.19) mg/g for associated plants in control plots, versus (11 ± 0.02) mg/g and (13.66 ± 1.57) mg/g in warmed plots. For 1-2 mm roots, values were (8.02 ± 0.66) mg/g and (8.29 ± 1.55) mg/g in control plots, versus (8.86 ± 0.02) mg/g and (8.19 ± 0.42) mg/g in warmed plots.

Warming had no significant effect on Chinese fir fine root nitrogen concentration ($P > 0.05$), but significantly increased nitrogen concentration in associated plant roots ($P < 0.05$).

[Figure 3: see original paper] Fig. 3 Root tissue nitrogen concentration by treatments and species for 0-1 mm and 1-2 mm diameter classes

3. Effects of Warming on Specific Root Respiration Rate

Warming treatment had no significant effect on specific root respiration (SRR) ($P > 0.05$), but species, diameter class, and their interaction significantly affected SRR ($P < 0.001$). For 0–1 mm roots, SRR was (10.16 ± 2.05) nmol O g ^{1} s ^{1} for Chinese fir and (9.19 ± 1.94) nmol O g ^{1} s ^{1} for associated plants in control plots, versus (11.95 ± 2.9) nmol O g ^{1} s ^{1} and (10.83 ± 1.04) nmol O g ^{1} s ^{1} in warmed plots. For 1-2 mm roots, values were (3.90 ± 0.58) nmol O g ^{1} s ^{1} and (5.42 ± 1.94) nmol O g ^{1} s ^{1} in control plots, versus (6.97 ± 2.28) nmol O g ^{1} s ^{1} and (4.76 ± 1.05) nmol O g ^{1} s ^{1} in warmed plots.

Warming had no significant effect on Chinese fir SRR ($P > 0.05$), but significantly decreased SRR in associated plants ($P < 0.01$), indicating that associated plant root respiration showed acclimation to warming while Chinese fir root respiration did not.

[Figure 4: see original paper] Fig. 4 Specific root respiration rate by treatments and species for 0-1 mm and 1-2 mm diameter classes

4. Effects of Warming on Fine Root Morphological Characteristics

Warming treatment and species had no significant effect on specific root length (SRL) ($P > 0.05$), but diameter class and the interaction between warming, species, and diameter class significantly affected SRL ($P < 0.001$). For 0-1 mm roots, SRL was (11.09 ± 1.76) m/g for Chinese fir and (18.26 ± 3.86) m/g for associated plants in control plots, versus (19.61 ± 4.86) m/g and (28.66 ± 8.96) m/g in warmed plots. For 1-2 mm roots, values were (4.99 ± 0.62) m/g and (8.83 ± 0.23) m/g in control plots, versus (5.55 ± 2.27) m/g and (5.45 ± 1.94) m/g in warmed plots.

Warming had no significant effect on Chinese fir SRL ($P > 0.05$), but significantly decreased SRL in associated plants ($P < 0.05$).

[Figure 5: see original paper] Fig. 5 Specific root length by treatments and species for 0-1 mm and 1-2 mm diameter classes

Warming treatment had no significant effect on specific root area (SRA) ($P > 0.05$), but species, diameter class, and the interaction between warming, species, and diameter class significantly affected SRA ($P < 0.001$). For 0-1 mm roots, SRA was (321.26 ± 51.93) cm^2/g for Chinese fir and (261.06 ± 85.69) cm^2/g for associated plants in control plots, versus (404.53 ± 13.30) cm^2/g and (477.57 ± 107.69) cm^2/g in warmed plots. For 1-2 mm roots, values were (176.77 ± 34.62) cm^2/g and (166.58 ± 53.04) cm^2/g in control plots, versus (356.55 ± 139.93) cm^2/g and (424.91 ± 118.97) cm^2/g in warmed plots.

Warming significantly increased SRA in both Chinese fir and associated plants ($P < 0.05$).

[Figure 6: see original paper] Fig. 6 Specific root area by treatments and species for 0-1 mm and 1-2 mm diameter classes

5. Effects of Warming on the Relationship Between Specific Root Respiration Rate and Specific Root Length

Specific root respiration rate (SRR) and specific root length (SRL) showed a highly significant power function relationship ($P < 0.001$). Covariance analysis revealed that warming treatment significantly affected both the intercept and slope of this relationship ($P < 0.01$), while species and the warming × species interaction had no significant effect ($P > 0.05$). This indicates that warming altered the balance between root maintenance cost and nutrient competition capacity, with no difference between Chinese fir and associated plants in how warming affected this relationship.

[Figure 7: see original paper] Fig. 7 Relationship between specific root length and specific root respiration rate for control (NW) and warming (WNW) treatments

** Table 6 Analysis of covariance for the effects of soil warming on the relationship between specific root respiration rate (SRR) and specific root length (SRL) for Chinese fir seedlings and associated plants**

1. Effects of Warming on Fine Root Biomass of Chinese Fir and Associated Plants

Fine root biomass largely reflects belowground investment by plants and represents their occupation of soil space and competitive ability for belowground resources. Warming significantly increased total 0–1 mm fine root biomass across all plants, contrasting with many previous warming studies that reported decreased fine root biomass [21–23]. For example, Bronson et al. [10] found that warming reduced live fine root biomass by 61.9% in black spruce, while Allen et al. [24] reported increased root biomass with temperature in orange trees (*Citrus aurantium*). Our study plants, including Chinese fir and associated species, were still in biomass accumulation stages. Warming may accelerate soil nitrogen mineralization, promoting plant growth. However, due to allometric constraints [19], increased soil nitrogen mineralization could reduce belowground carbon allocation in stable ecosystems, decreasing fine root biomass. In growing systems, accelerated nitrogen mineralization may enhance overall plant biomass, including fine roots.

Most previous warming studies focused on single species without distinguishing among species [15–17]. Our study revealed that although warming increased total fine root biomass, the trends differed between Chinese fir and associated plants. Under elevated soil temperature, Chinese fir 0–1 mm fine root biomass significantly decreased while associated plant fine root biomass significantly increased. This asymmetric response suggests that soil warming affects competition differently between species. The increase in associated plant aboveground biomass after warming, compared to non-significant changes in Chinese fir, further implies that competition from other plants may intensify in Chinese fir plantations under global warming. Effective weed control measures may become increasingly important for Chinese fir plantation management.

2. Effects of Warming on Fine Root Nitrogen Concentration

The 0–1 mm diameter class represents the most active portion of plant root systems for water and nutrient absorption [25]. Soil temperature is a key factor affecting plant growth. Warming significantly increased tissue nitrogen concentration in associated plants ($P < 0.05$), consistent with many studies [26–27], but had no significant effect on Chinese fir fine root nitrogen concentration. This difference may relate to warming effects on soil nutrients and competitive abilities among species. Temperature strongly influences soil organic matter decomposition and nutrient mineralization [28-29]. Increased soil temperature accelerates nitrogen mineralization rates, enhancing available nutrients. Plant root nutrient uptake capacity typically correlates positively with soil temperature [30]. In this study, warming increased soil nitrogen mineralization, promoting nutrient uptake by associated plants and significantly increasing their root tissue nitrogen concentration.

The lack of significant change in Chinese fir root nitrogen concentration may reflect competitive differences. The associated plants in our warming plots were primarily pioneer species such as *Helicteres angustifolia* and *Mallotus lianus*, which are adapted to open environments with rapid early growth and strong nutrient acquisition capabilities. These species could quickly capture increased soil nutrients from warming, leading to higher tissue nitrogen concentrations. In contrast, Chinese fir may be less competitive, preventing significant nitrogen accumulation. Notably, soil ammonium and nitrate concentrations in warmed plots were not significantly higher than controls, likely because mineralized nitrogen was rapidly absorbed by associated plant roots. This differs from our parallel study without associated plants, where warming significantly increased soil nitrogen availability and Chinese fir root nitrogen concentration [32], suggesting that competition determines nutrient distribution under warming.

3. Effects of Warming on SRL, SRA, and SRR

Specific root length (SRL) and specific root area (SRA) are key morphological indicators reflecting nutrient absorption efficiency per unit root biomass. Under warming, Chinese fir SRL showed no significant change, while associated plant SRL significantly decreased ($P < 0.05$). This pattern resembles Björk et al.' s [33] findings in Swedish dry tundra, where warming decreased SRL in dry heath shrubs but not in dry meadow communities. When nutrients are abundant, plants may reduce investment in root length and surface area while accumulating soluble nitrogen in tissues. However, Chinese fir facing strong competition may need to increase surface area to acquire sufficient nutrients, explaining its increased SRA under warming.

Specific root respiration rate reflects maintenance costs for resource absorption. Many studies report decreased fine root respiration after warming [15], with species varying in acclimation capacity [34-37]. Our results show that associated plant SRR significantly decreased under warming ($P < 0.01$), indicating respiratory acclimation, while Chinese fir SRR showed no significant change, suggesting no acclimation. This acclimation would reduce maintenance costs and enhance competitiveness of associated plants under warming.

Root respiration is closely linked to morphology [14, 25]. We found a highly significant power function relationship between SRR and SRL ($P < 0.001$), consistent with studies on *Quercus serrata* and other species [25]. Warming significantly affected both the slope and intercept of this relationship ($P <$

0.01), while species had no significant effect, indicating that warming altered the balance between maintenance cost and competition capacity similarly for both Chinese fir and associated plants.

5. Conclusion

Compared with Chinese fir, associated plants gained competitive advantages for belowground resources under warming conditions. They significantly increased total fine root biomass to capture accelerated soil nutrient mineralization, while reducing per-unit-mass maintenance costs through decreased SRL, increased SRA, and respiratory acclimation, thereby enhancing adaptability to global warming. Chinese fir, however, was disadvantaged by reduced total fine root biomass and lacked respiratory acclimation. To compensate, Chinese fir increased SRL and SRA, but this increased per-unit-mass maintenance costs, indicating lower adaptability to global warming. These results suggest that competition from associated plants may intensify in Chinese fir plantations under global warming, making effective weed control increasingly important for plantation management.

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Note: Figure translations are in progress. See original paper for figures.