Stem CH_4 emissions from the reclaimed forests: magnitude, drivers, and contribution

Mengyu Ge[1,2,3], Min Tan[4*] and Yang Liu[5]

Abstract

Background Trees in natural forests are a major contributor to atmospheric methane (CH_4), yet these emissions have never been investigated in reclaimed forests. Our study aimed to assess the magnitude, seasonality, drivers, and contributions of tree CH_4 emissions to ecosystem CH_4 flux in the reclaimed forests. We measured CH_4 emissions from different emission pathways, including the stems of trees (*Populus euramericana*, *Metasequoia glyptostroboides*, and *Camphora officinarum*), shoots of herbs (*Carex breviculmis* and *Carex dispalata*), and soils in the two reclaimed forests with reclamation periods of 12 and 5 years. We identified factors controlling seasonal tree CH_4 emissions and measured tree morphological variables (diameter at breast height, wood density, and lenticel density) to determine species differences in emissions.

Results CH_4 emissions from trees in the 12-year-old reclaimed forest were significantly higher than those in the 5-year-old forest. Seasonal variations in tree CH_4 emissions were primarily driven by growth stage and soil parameters, including soil CH_4 flux, temperature, and moisture.

Conclusion In the reclaimed forests, tree-mediated CH_4 emissions could be an important contributor to ecosystem CH_4 flux, with contributions varying by season. As these forests mature and become ecologically restored, they may significantly impact regional and global CH_4 emissions.

Keywords Driver, Contribution, Reclaimed forest, Seasonal variation, Tree-mediated CH_4 emission

Introduction

Methane (CH_4) is crucial in mitigating climate change due to its high global warming potential, short atmospheric lifetime, diverse sources, and contributions to the feedback mechanism that amplify climate change (Geum et al. 2024; Zhang et al. 2023). Forests are dynamic systems that can function as both sources and sinks of atmospheric CH_4, depending on various factors, e.g., soil conditions, tree species, atmospheric conditions, and human activities (Feng et al. 2023; Guo et al. 2023). The estimation of the forest CH_4 budget still involves substantial uncertainty (Dlugokencky et al. 2011; Zhou et al. 2021b), hindering accurate assessment of ecosystem feedback to climate change. To address this issue, it is essential to develop a comprehensive understanding of the magnitude and contributions of different emission pathways.

The net effect of forest soils on the CH_4 budget is the balance between CH_4 production and consumption. Forest soils have properties like well-developed structure with high porosity, high amount of organic matter, balanced soil moisture level, as well as diverse and abundant methanotrophic bacteria, collectively creating an optimal environment for methanotrophic bacteria to thrive

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and efficiently oxidize CH_4 (Lee et al. 2023; Lohila et al. 2016; Wang et al. 2016; Zhou et al. 2021a). Therefore, forest soils have a higher potential for CH_4 consumption compared to other ecosystems and represent a significant CH_4 sink in the global CH_4 budget (Song et al. 2024; Wu et al. 2020).

Herbaceous plants (hereafter 'herbs') with aerenchyma tissues—air-filled spaces that facilitate gas transport and emission—can efficiently transport soil-produced CH_4 to escape into the atmosphere, bypassing CH_4 oxidation in aerobic soil layers (Ge et al. 2023). This pathway has been extensively studied in various ecosystems, including wetlands, peatlands, and rice paddies (Ding et al. 2005; Garnett et al. 2020; Wang et al. 1997), since the pioneering work of Sebacher et al. (1985), which investigated CH_4 emissions from diverse wetland aquatic plants. These studies reveal that herb-mediated CH_4 emissions are affected by a combination of abiotic factors (e.g., watertable level, porewater CH_4 concentration, temperature, solar radiation, humidity, and soil properties) and biotic factors (e.g., species, phenology, biomass, stomatal conductance, transpiration, and root length and permeability). Herb-mediated CH_4 emissions have been found to mediated over 90% of ecosystem CH_4 emissions and significantly reduce porewater CH_4 concentration in soils (Dise 1993; Whiting and Chanton 1992).

In contrast, tree-mediated CH_4 emissions are the least studied pathway, despite recent findings confirming their significant role in ecosystem CH_4 flux. Trees influence soil properties as well as the abundance and activities of microbes, thereby affecting CH_4 production, oxidation, and emissions (Putkinen et al. 2021; Turetsky et al. 2014). Additionally, soil-produced CH_4 can diffuse into roots and move through plant tissues via intercellular spaces, aerenchyma, and the transpiration stream in xylem, eventually being emitted from barks, cracks, lenticels in stems and stomata (small leaf openings for gas exchange) on leaves (Anttila et al. 2024; Moisan et al. 2024; Pangala et al. 2015; Pangala et al. 2013). Recent studies indicate that the contribution of tree-mediated CH_4 emissions to ecosystem flux vary over time (Han et al. 2022; Pangala et al. 2015). However, the number of studies assessing tree-mediated CH_4 emissions compared to other gas emission pathways (e.g., soils and herbaceous plants) in forest ecosystems are limited. Moreover, existing studies on tree-mediated CH_4 emissions are typically short-term, potentially biasing the estimation of annual CH_4 flux. To properly interpret CH_4 fluxes in the soil–tree–atmosphere continuum, seasonal measurements with environmental observations are imperative.

Another aspect of tree-mediated CH_4 emissions that should be noted is that a wider range of tree species should be measured. Research investigating CH_4 fluxes from multiple tree species at the same site and under identical environmental conditions has highlighted significant variations in emission magnitude, vertical distribution, and temporal patterns (Pangala et al. 2015; Vainio et al. 2022). These species-specific differences in tree CH_4 emissions could be attributed to variations in wood density, diameter, bark structure, root distribution (Covey and Megonigal 2019), stomatal conductance, cuticle permeability (Garnet et al. 2005), lenticel density (Pangala et al. 2013), presence of aerenchyma, adventitious roots, pneumatophores (Zhang et al. 2022), and interactions with microbes within trees or in soils (Putkinen et al. 2021). To date, only a few tree species have been investigated, which hinders accurate estimation of total CH_4 emissions from forests.

Most research has investigated tree-mediated CH_4 emissions in natural forests (Halmeenmäki et al. 2017; Jeffrey et al. 2021; Machacova et al. 2023; Mander et al. 2022), while studies in reclaimed forests are scarce. Coal mining significantly contributes to global land degradation, leading to severe land subsidence issues (Lechner et al. 2016). Many efforts have been made to reclaim subsided lands through reforestation and ecological restoration to improve environmental conditions and mitigating mining impacts (Holl et al. 2022; Miao and Marrs 2000). Reclaimed forests, unlike natural forests, often have unique soil and hydrological conditions due to their disturbance history and reclamation processes (Buta et al. 2019; Tarnawczyk et al. 2021). Restoring soils to a state similar to natural conditions is complex and time-consuming, often taking several decades (Lal 2015; Ma et al. 2022). Changes in soil and hydrological conditions in reclaimed forests, and the duration since reclamation, potentially could result in different CH_4 dynamics compared to natural forests. However, the magnitude, variations, and drivers of tree-mediated CH_4 emissions in reclaimed forests remain understudied.

In this study, we measured CH_4 emissions from the stems of trees (*Populus euramericana*, *Metasequoia glyptostroboides*, and *Camphora officinarum*), shoots of herbs (*Carex breviculmis* and *Carex dispalata*), and soils. The measurement was conducted in the 5-year-old and 12-year-old reclaimed forests, located approximately 3 km apart. Our goal was to assess the magnitude, seasonal variations, and drivers of tree-mediated CH_4 emissions, and to quantify their contribution to total CH_4 flux alongside with other emission pathways, including herb-mediated and soil CH_4 emissions. We hypothesized that: (i) the reclaimed period would significantly affect stem CH_4 emissions; (ii) stem CH_4 emissions would vary seasonally due to variations in environmental conditions and tree growth stages; (iii) stem CH_4 emissions would vary significantly between tree species due to morphological

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differences; and (iv) trees could contribute significantly to ecosystem CH_4 flux.

Materials and methods
Site description
The measurement was conducted in the Longdong mining area (116.86°E, 34.91°N), west of Weishan Lake, China. The annual mean temperature in the area is of 14.2 °C, and precipitation is 816.4 mm, with a temperate semi-humid monsoon climate. The Longdong Coal Mine, constructed in 1982 and operational since 1987, spans around 24.95 km^2 with an annual production capacity of 30 million tons. Long-term coal mining activities have caused significant environmental issues, e.g., land abandonment, subsidence, and degradation. To restore the ecological environment and enhance land use efficiency, reforestation programs have been implemented in the Longdong mining area.

We selected two reclaimed forests with reclamation periods of 12 and 5 years, respectively, to study the effects of reclamation period on stem CH_4 emissions. The distance between the two forests was around 3 km. The plant communities in both forests was similar, dominated by trees *Populus*, *Betula*, *Ulmus*, *Camphora*, *Metasequoia*. The forest understorey was dominated by sedges *Carex breviculmis* and *Carex dispalata*, with grass *Imperata cylindrica* and *Pentanema vestitum* also present. The water-table level was relatively high and greatly influenced by seasonal precipitation and hydrological regulation.

CH_4 flux measurement
In each forest, measurements were conducted across three plots, providing three within-forest replicates per plant species. This setup resulted in a total of 18 trees being measured in these two reclaimed forests. We conducted the measurement quarterly in April, July, October in 2023 and January in 2024 to investigate the effects of plant development, senescence, and dormancy (collectively called 'plant phenology') on stem CH_4 emissions. Each measurement campaign lasted around 2 weeks, with CH_4 flux measured only during the daytime.

We measured CH_4 flux from the stems of *Populus euramericana*, *Metasequoia glyptostroboides* and *Camphora officinarum* using the chamber (20.5×13.4×6.8 cm) described by Han et al. (2022), hereafter called 'stem chamber' (Fig. 1). The stem chamber, made of transparent polypropylene, consisted of a chamber body and base. We installed the stem chamber base at different heights on the tree (0.5, 1.0, and 1.5 m above the ground) using silica gel.

CH_4 fluxes from the shoots of the herbs *Carex breviculmis* and *Carex dispalata* were measured using the 'herb chamber' (Fig. 1). This chamber comprised two plexiglass plates and a transparent chamber body (volume: 0.00056 m^3) made of polymethyl methacrylate. During each
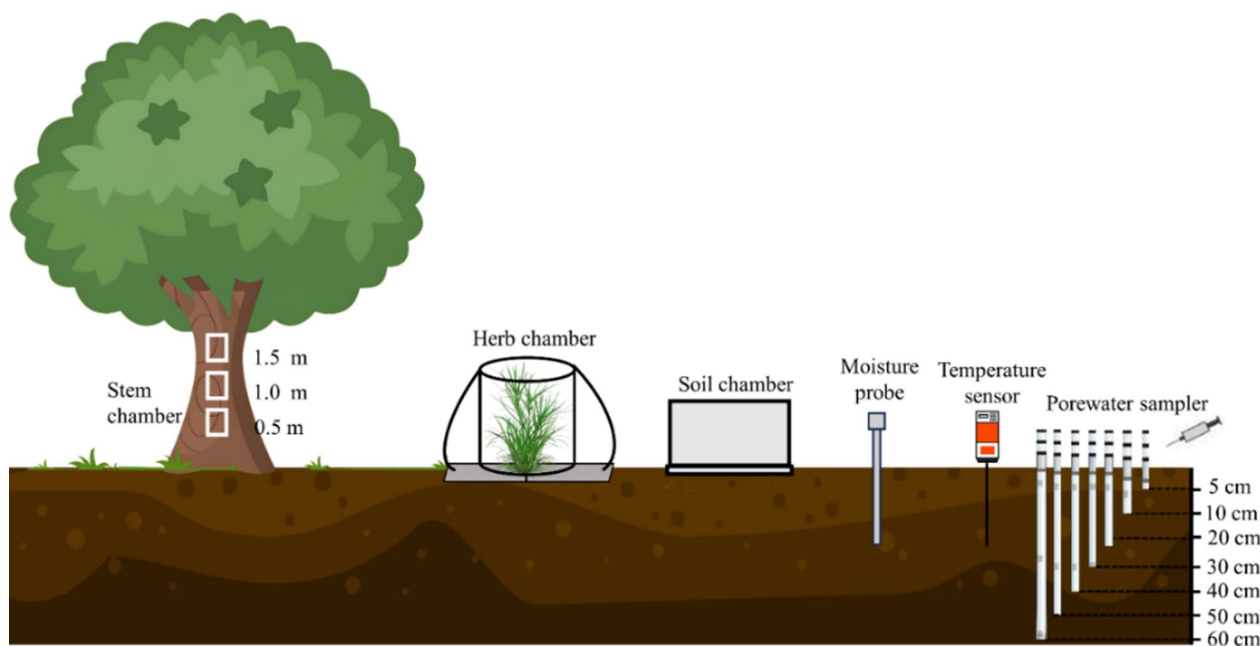
Fig. 1 Diagram illustrating the experimental design. Observations of CH_4 flux from tree stems at three heights (0.5, 1.0, 1.5 m), herbaceous plants, and soils. Observations of soil parameters, including soil temperature, soil water content, and porewater CH_4 concentration at seven depths (5, 10, 20, 30, 40, 50, 60 cm)

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measurement, the shoots were placed between the plexiglass plates, and the chamber was positioned on top to cover them. Airtightness was achieved by placing a rubber seal between the chamber bottom and the plates, and by pressing the chamber against the plates with a metal spring attached to the sides of the plates. After each flux measurement campaign, the herb sample enclosed in the chamber was clipped to measure the single-sided leaf area. For more detailed descriptions, see Korrensalo et al. (2022).

CH$_4$ fluxes from bare soils were measured using the 'soil chamber' (Fig. 1) described by Zhang et al. (2020). This chamber comprised a stainless-steel base frame and a chamber body ($60\times60\times40$ cm). The chamber base was inserted vertically into soils to a depth of 10 cm to ensure a gas-tight seal. This was done two weeks before the measurement to allow soil and microbes to stabilize after the disturbance caused by the insertion. During the measurement, the chamber body was securely positioned on the base frame with rubber seals applied to the chamber body bottom to enhance the airtightness.

All chamber bodies were equipped with ports for gas outlet and inlet tubes and fans for mixing headspace air. CH$_4$ fluxes were measured by closing the chamber for 4 min, during which the headspace gas was continuously circulated between the closed chamber and the analyser (LGR-UGGA, Los Gatos Research, USA) using polytetrafluoroethylene (PTFE) tubes. Simultaneously, we recorded environmental variables, including air temperature, relative humidity, soil temperature and water content at the depth of 30 cm. We focused on the depth of 30 cm because temperature, moisture, and microbial activity at this depth tend to be relatively stable and representative of broader soil conditions influencing CH$_4$ dynamics (Davidson et al. 2002).

CH$_4$ flux was determined based on the linear change of CH$_4$ concentration over the closure period (dC/dt, Eq. 1):

$$F = \frac{dC}{dt} \cdot \frac{MPV}{RT} \cdot 3600 \tag{1}$$

where F is CH$_4$ flux; M is the molar mass of CH$_4$ (16,042 mg); P is the atmospheric pressure (101,325 Pa); V is the chamber volume (m^3); R is the gas constant (8.3144598 J K^{-1} mol^{-1}); T is the chamber temperature (K).

Porewater CH$_4$ concentration

Porewater samples were collected daily during each measurement campaign from samplers installed at seven depths (5, 10, 20, 30, 40, 50, 60 cm) in each of the three plots within the two forests. Each sampler was constructed from PTFE tubing with a perforated bottom end wrapped in a nylon mesh for filtering soil particles.

The top end of the tube was fitted with a three-way gastight valve, allowing us to sample 10 ml porewater at the specific depth using a 20 ml syringes. Then, the syringe was filled with 10 ml synthetic air and shaken for 5 min, allowing the dissolved CH$_4$ to equilibrate between the water and headspace. The gas sample was subsequently transferred from the syringe to a 12 ml vial, and CH$_4$ concentration of the gas was measured by a gas chromatograph. For more detailed instructions, see Ge et al. (2023).

Tree measurements

Diameter at breast height (DBH) was measured at 1.3 m above the ground. Lenticel density was estimated by counting the number of lenticels within 2×2 cm grids placed at stem heights of 0.5 and 1.5 m. The stem lenticle referred exclusively to normal lenticels, as no hypertrophied lenticels were detected. Wood samples were extracted at 1.3 m height using an increment borer with an internal diameter of 5.15 mm, manufactured by Haglöf Sweden (Längsele, Sweden). Wood volume and dry mass of the samples were calculated to determine wood density, following Pangala et al. (2013). All tree measurements were conducted in the 12-year-old reclaimed forest during summer 2023 after the flux measurement campaign.

Partitioning of CH$_4$ flux

The measured stem area-based CH$_4$ flux was upscaled to per land surface area to estimate the proportion of tree-mediated CH$_4$ emissions to the total CH$_4$ flux. We assumed the stem below 1.75 m was a cylinder and divided it into three sections: 0–0.75 m, 0.75–1.25 m, and 1.25–1.75 m. This approach allowed us to calculate tree CH$_4$ flux between 0 and 1.75 m height by multiplying stem area-based CH$_4$ flux at the specific height by the corresponding surface area of each cylindrical section (Eq. 2). The tree-mediated CH$_4$ emissions were then upscaled to the stand level by multiplying the calculated tree CH$_4$ flux by the stand density of trees (Eq. 3).

$$F_{tree} = F_a \times S_a + F_b \times S_b + F_c \times S_c \tag{2}$$

$$F_{stand} = F_{tree} \times D_{stand} \tag{3}$$

where F_{tree} is the tree CH$_4$ flux between the height of 0 and 1.75 m (µg tree^{-1} h^{-1}); F_a, F_b, and F_c are stem CH$_4$ flux at the height of 0.5, 1.0, and 1.5 m, respectively; S_a, S_b, and S_c are surface area of the cylinder Sects. 0–0.75 m, 0.75–1.25 m, and 1.25–1.75 m, respectively; D_{stand} represents the stand density of trees (trees ha^{-1}).

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Statistical analysis

The data analysis was performed in R v3.6.1 (R Core Team 2019). The significance of the stem CH_4 emissions between seasons and species, as well as seasonal variations in porewater CH_4 concentration, were analysed using ANOVA and Tukey tests. The dataset was divided into four time periods by measurement campaigns: spring, summer, autumn, and winter. Plant phenology was denoted by the variable 'season' in Table 1. The linear-mixed effect model was applied to assess the relative importance of phenology and environmental variables on seasonal variations in stem CH_4 emissions. Fixed effects were season, air temperature, relative humidity, soil temperature and water content at depth of 30 cm, while sample id and forest site were random effects.

Results

Temporal and spatial variations in stem CH_4 emissions

Throughout the observations, trees in the 12-year-old and 5-year-old reclaimed forests released significant quantities of CH_4 (Fig. 2), even during winter dormancy. The stem CH_4 emissions from both forests exhibited similar seasonal variations, peaking in summer, with means of 456 and 245 µg m^{-2} h^{-1}, respectively. The emissions significantly decreased in autumn, with means of 197 and 75 µg m^{-2} h^{-1}, respectively. The lowest emissions were observed in winter, 18 and 14 times smaller than those in summer, respectively. Overall, stem CH_4 emissions were higher in the 12-year-old forest than that observed in the
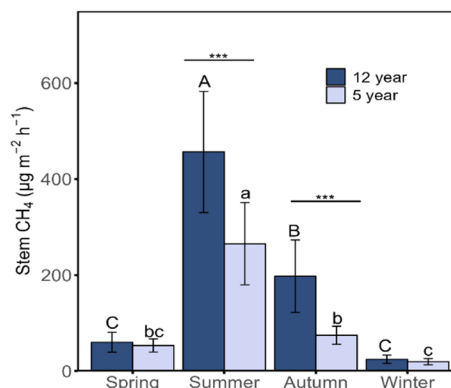
Fig. 2 Seasonal variations in the stem CH_4 emissions (µg m^{-2} stem area h^{-1}) in the 12-year-old and 5-year-old reclaimed forests. Error bars denote standard deviation. Uppercase and lowercase letters represent the significant difference ($P < 0.05$) of the stem CH_4 emissions between seasons in the 12-year-old and 5-year-old reclaimed forests, respectively, as determined by ANOVA and Tukey tests. Asterisks denote the significance of the stem CH_4 emissions between the two forests in the same season (***, $P < 0.001$)

5-year-old forest, with significant differences occurring in summer and autumn ($P < 0.001$ for both).

The linear-mixed effect model accounted for 69% of the variations in the stem CH_4 emissions (Table 1). The fixed effects, including measurement season, air temperature, relative humidity, soil temperature and water content at the dept of 30 cm, explained 57% of the variations. The stem CH_4 emissions significantly increased in summer when trees were in fast growth period, and the emissions had positive correlation with higher soil temperature and water content (all $P < 0.05$, Table 1, Fig. 3). However, atmospheric parameters air temperature and relative humidity did not significantly affect stem CH_4 emissions.

Seasonal variations in environmental conditions

Daily mean air temperature varied seasonally, ranging from −2 to 35 °C throughout the observations (Fig. 4a). It peaked in summer, reached the lowest in winter, and remained at similar levels in spring and autumn. Soil temperature at the depth of 30 cm (ranging from 2 to 30 °C) and relative humidity (ranging from 53 to 81%) showed a seasonal pattern closely resembling that of air temperature (Fig. 4b, c). For soil water content at the depth of 30 cm, it was higher in autumn compared to other seasons (Fig. 4d).

Porewater CH_4 concentration differed between the two forests and varied significantly with soil depth (Fig. 5). Overall, it was higher in the 12-year-old reclaimed forest compared to the 5-year-old reclaimed forest. In both forests, the highest and lowest porewater CH_4 concentration were observed at depths 30 and 10 cm, respectively.

Table 1 Summary statistics for the linear-mixed effect model fitted to the stem CH_4 emissions with fixed effects of season, air temperature, relative humidity, soil temperature and water content at the depth of 30 cm, and with random effects of sample ID and forest site

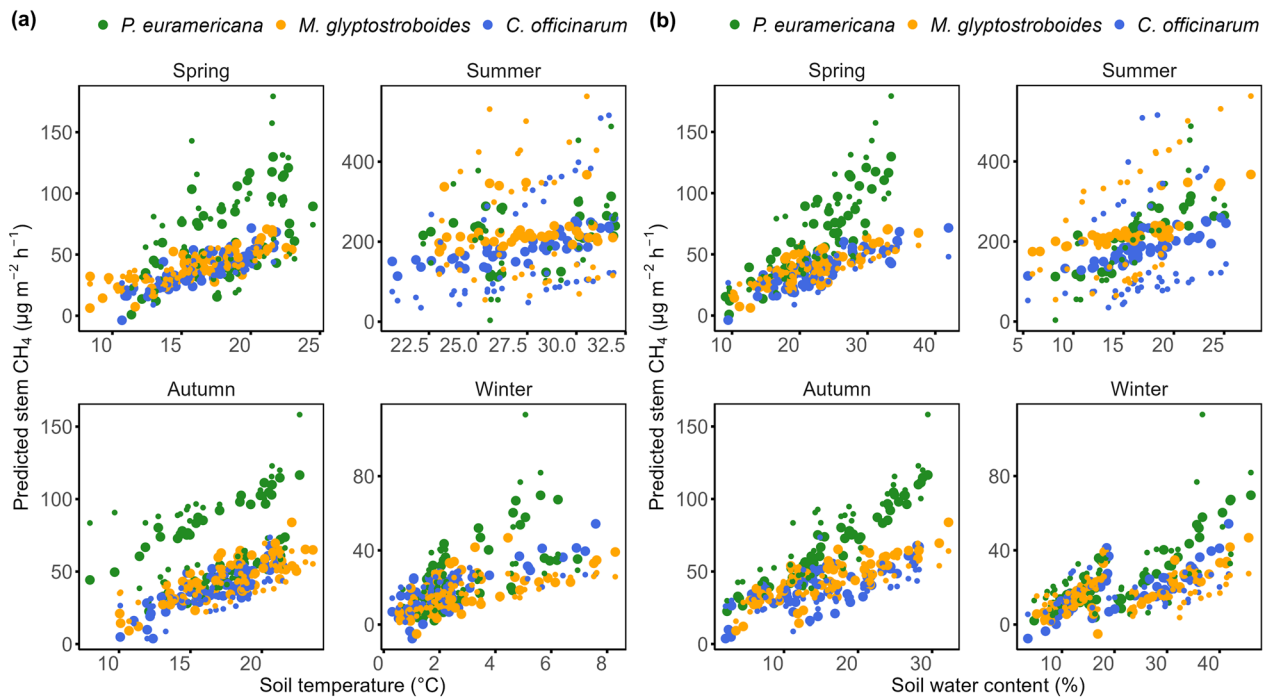| Predictors	Estimates	SE	*P* value
Fixed part			
Constant (Spring)	53.07	30.26	0.08
Season (Summer)	137.18	20.72	< 0.001***
Season (Autumn)	15.46	12.54	< 0.05*
Season (Winter)	− 36.36	22.39	< 0.01**
Air temperature	0.93	0.51	0.07
Soil temperature	3.34	1.18	0.001**
Relative humidity	− 0.26	0.34	0.45
Soil water content	1.88	0.52	< 0.001***
Random part			
SD (Sample ID)	6.2		
Forest site	1.2		
Residual SD	4.8		
Marginal R^2/Conditional R^2	0.57/0.69		

Season is an indicator of tree phenology, divided into spring, summer, autumn, and winter. *P* values denote statistical significance: *0.05; **0.01; ***0.001

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Fig. 3 The effects of soil temperature (**a**, ℃) and soil water content (**b**, %) at the depth of 30 cm on the predicted stem CH_4 emissions (µg m^{-2} stem area h^{-1}), fitted with the linear-mixed effect model. Predicted stem CH_4 emissions are shown to account for variability and integrate multiple influencing variables, providing clearer relationships than raw data
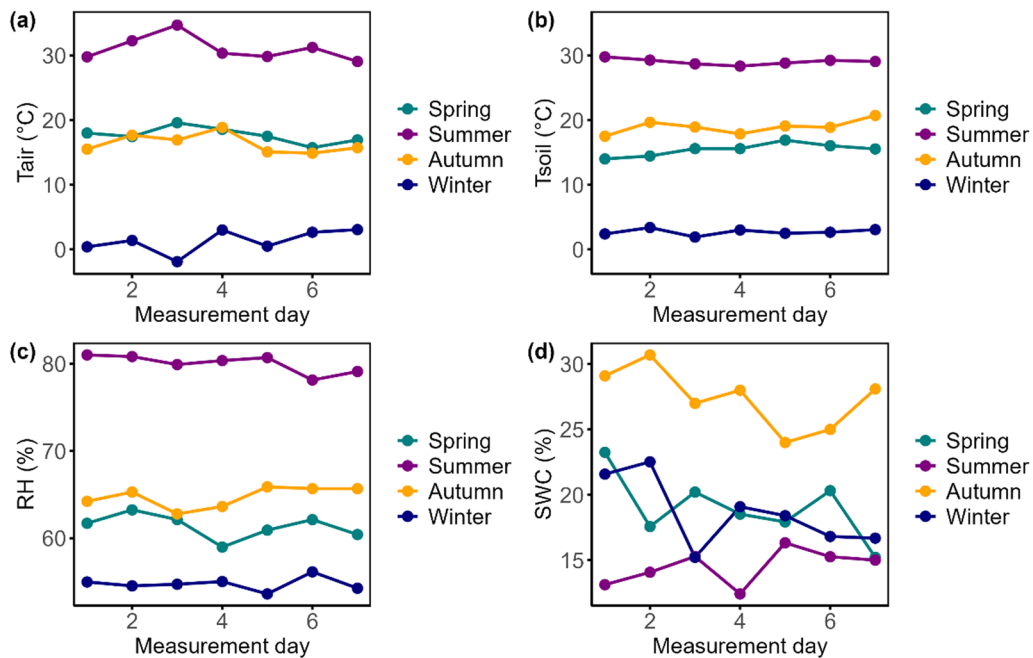
Fig. 4 Daily mean air temperature (**a**, ℃), soil temperature at the depth of 30 cm (**b**, ℃), relative humidity (**c**, %), and soil water content at the depth of 30 cm (**d**, %)
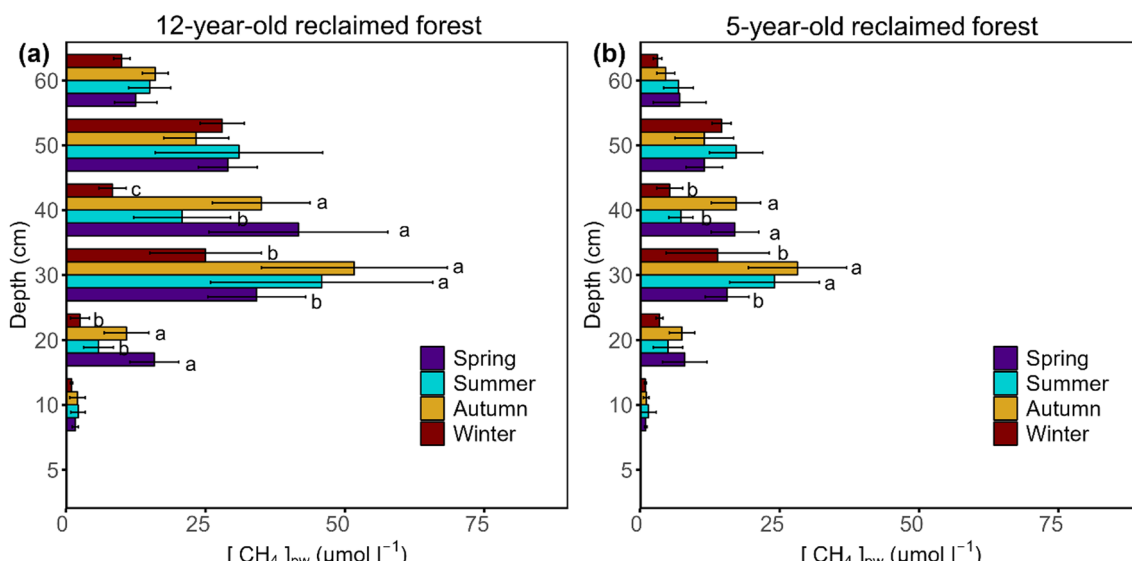
Fig. 5 Porewater CH_4 concentration ($[CH_4]_{pw}$, µmol l^{-1}) measured at seven soil depths (5 to 60 cm below the soil surface) in the 12-year-old (**a**) and 5-year-old (**b**) reclaimed forests. Letters above bars denote significant differences ($P < 0.05$) between seasons by using ANOVA and Tukey tests
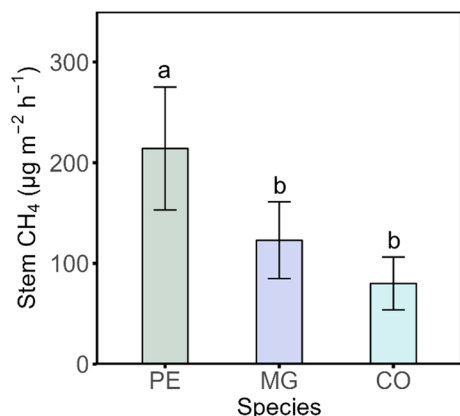
Fig. 6 The mean stem CH_4 emissions (µg m^{-2} stem area h^{-1}) from *Populus euramericana* (PE), *Metasequoia glyptostroboides* (MG), and *Camphora officinarum* (CO) throughout the observations. Letters above bars denote significant differences ($P < 0.05$) between species by using ANOVA and Tukey tests

Additionally, in the 12-year-old forest, porewater CH_4 concentration varied seasonally between depths of 20 and 40 cm, while these variations occurred between depths of 30 and 40 cm in the 5-year-old forest.

Species-specific stem CH_4 emissions

The stem CH_4 emissions varied between tree species (Fig. 6). *P. euramericana* showed the highest stem CH_4 emissions, with a mean of 214 µg m^{-2} h^{-1} throughout the observations. It had the largest DBH and lenticel density, and its wood density was intermediate between that of *M. glyptostroboides* and *C. officinarum* (Table 2). The stem CH_4 emissions of *M. glyptostroboides* and *C. officinarum* were similar, with means of 123 and 80 µg m^{-2} h^{-1}, respectively. *M. glyptostroboides* had the smallest DBH and wood density, while *C. officinarum* had the largest wood density and smallest lenticel density.

Table 2 The diameter at breast height (DBH), wood density, and lenticel density of *Populus euramericana*, *Metasequoia glyptostroboides* and *Camphora officinarum*

Species	DBH (cm)	Wood density (g cm^{-3})	Lenticel density (cm^{-2})
Populus euramericana	25.1 ± 2.4	0.35 ± 0.015	1.71 ± 0.15
Metasequoia glyptostroboides	20.2 ± 1.5	0.31 ± 0.023	0.85 ± 0.11
Camphora officinarum	23.4 ± 2.1	0.55 ± 0.018	0.61 ± 0.04

The data are collected from the selected trees used in this study

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Partitioning of ecosystem CH₄ flux

The relative contributions of each CH_4 emission pathway to the total ecosystem CH_4 flux varied seasonally, with an overall consistent pattern observed in both the 12-year-old and 5-year-old reclaimed forests (Table 3, Fig. 7) Tree-mediated CH_4 emissions, estimated based on the lowest 1.75 m of stem, ranged from 0.69 to 13.85 $\mu g\ m^{-2}$ land surface h^{-1}, throughout the observations. A higher proportion of this pathway was observed in spring and winter, with values of 63% and 65%, and 47% and 67% for the 12-year-old and 5-year-old reclaimed forests, respectively. In contrast, tree-mediated CH_4 emissions accounted for less than 2% of the total ecosystem CH_4 flux in summer and autumn when herb-mediated CH_4 emissions were the dominant pathway. Soil-mediated CH_4 emissions showed less seasonal variation compared to other pathways, contributing approximately 25% throughout the observations.

Discussion

The magnitude of stem CH₄ emissions

The stem CH_4 emissions from the 12-year-old reclaimed forest ranged from 30 to 537 $\mu g\ m^{-2}\ h^{-1}$, similar to those observed in natural, undisturbed upland forests (Han et al. 2022; Wang et al. 2016). This similarity implies that the 12-year-old reclaimed forest has developed soil and vegetation characteristics comparable to those found in natural upland forests, indicating successful ecological restoration. In contrast, the stem CH_4 emissions from the 5-year-old reclaimed forest were significantly lower compared to those observed in the 12-year-old reclaimed forest, probably owing to its less matured state and reduced stability compared to natural forests. The short recovery time from mining and reclamation process may have led the 5-year-old forest to have more aerobic soils with lower organic matter and less active microbial activities (Hu et al. 2020; Sheoran et al. 2010), resulting in a notably

Table 3 CH_4 emissions from trees, herbs, and soils at the stand level (mean ± standard deviation) and their contributions to the total ecosystem CH_4 emissions in the 12-year-old and 5-year-old reclaimed forests

Season	Reclamation period	Ecosystem CH₄ emissions ($\mu g\ m^{-2}$ land surface h^{-1})			
		Tree	**Herb**	**Soil**	**Total flux**
Spring	12 Years	2.80 ± 0.57 (62.84%)	0.7 ± 0.23 (15.70%)	0.96 ± 0.13 (21.46%)	4.46 ± 0.93
Summer	12 Years	13.85 ± 2.66 (1.22%)	881 ± 293.71 (77.92%)	235 ± 42.62 (20.86%)	1130.84 ± 338.99
Autumn	12 Years	3.07 ± 1.39 (1.54%)	176 ± 51.83 (88.58%)	19.65 ± 3.43 (9.88%)	198.95 ± 56.65
Winter	12 Years	1.08 ± 0.45 (65.14%)	0.01 ± 1E-03 (0.54%)	0.57 ± 0.12 (34.32%)	1.66 ± 0.58
Spring	5 Years	1.48 ± 0.27 (47.21%)	0.55 ± 0.08 (17.60%)	1.10 ± 0.24 (35.20%)	3.13 ± 0.59
Summer	5 Years	8.33 ± 2.29 (1.20%)	481 ± 67.83 (69.58%)	202 ± 42.62 (29.22%)	691.33 ± 112.74
Autumn	5 Years	1.63 ± 0.27 (1.68%)	80.17 ± 18.50 (82.82%)	15.00 ± 3.43 (15.50%)	96.8 ± 22.21
Winter	5 Years	0.69 ± 0.11 (67.00%)	0.01 ± 1E-03 (0.97%)	0.34 ± 0.06 (32.99%)	1.03 ± 0.71
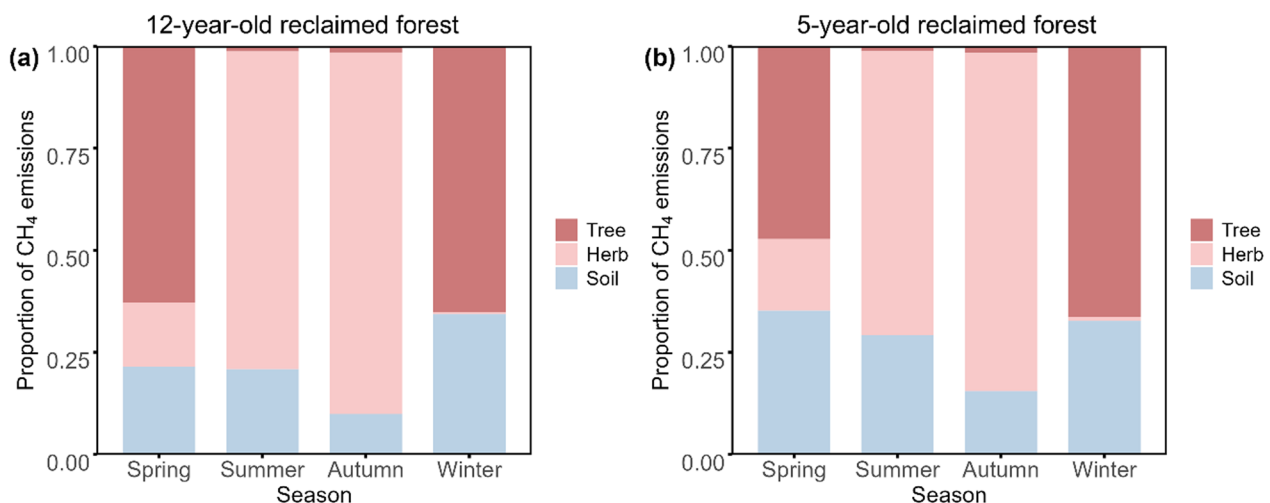
Fig. 7 The contribution of different emission pathways (trees, herbs, and soils) to the ecosystem CH_4 flux in the 12-year-old (**a**) and 5-year-old (**b**) reclaimed forests

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lower porewater CH_4 concentration (Fig. 5). Overall, our results suggest that reclaimed forests, once sufficiently matured and ecologically restored, could significantly contribute to regional and global CH_4 emissions.

Seasonality and drivers of stem CH_4 emissions

The stem CH_4 emissions observed in our study showed a seasonal pattern similar to that observed in natural forests (Han et al. 2022; Pangala et al. 2015; Zhang et al. 2022). Our results imply the importance of tree phenology (the 'season' variable in Table 1) in controlling stem CH_4 emissions. During periods of rapid growth, trees exhibit higher photosynthetic activity, releasing more substrates that enhance CH_4 production in the rhizosphere (Machacova et al. 2023). If the trees we investigated mainly transported gas with xylem sap flow, increasing transpiration in summer could facilitate the transport of dissolved gas (Anttila et al. 2024). Additionally, if the in-plant CH_4 production could occur in these trees, as found in *Populus* (Feng et al. 2022), elevated physiological activities in summer could increase non-structural carbohydrates and decrease oxygen availability, enhancing microbial CH_4 production and concentration in the wood (Li et al. 2020). Furthermore, the detectable stem CH_4 emissions in winter implies the ongoing microbial CH_4 production and gas diffusion, despite low soil temperature and moisture. Therefore, conducting tree flux measurements in winter is crucial to accurately estimate CH_4 budget in reclaimed forests.

Our results demonstrate that soil parameters such as soil CH_4 flux, temperature, and water content could significantly affect stem CH_4 emissions (Figs. 3, S1), consistent with previous studies (Han et al. 2022; Sjögersten et al. 2020; Terazawa et al. 2021; Vainio et al. 2022). While low soil moisture in winter typically reduces CH_4 production and could increase CH_4 uptake due to enhanced methanotrophic activity (Nazaries et al. 2013), the CH_4 emissions we observed under these conditions instead of the expected uptake can be attributed to several overriding factors. First, gas transport mechanisms may facilitate the rapid movement of CH_4 from deeper soil layers or within the tree, bypassing zones where methanotrophy typically occurs (Maier et al. 2018; Megonigal et al. 2020). Second, the methanotrophic microbial community might be less active or less abundant in the reclaimed forest due to site-specific conditions, such as soil chemistry or compaction, that inhibit methanotrophic bacteria (Epron et al. 2016; Smith et al. 2003). This effect might be further exacerbated by lower winter temperatures, which can slow methanotrophic activity more significantly than methanogenesis, particularly if methanogens were more cold-tolerant or resided in insulated microenvironments (Conrad 2023). Third, in-plant CH_4 production

may be stimulated under low soil moisture conditions due to the reduced hydraulic connectivity and increased water stress, which can limit O_2 transport within the tree and create anaerobic zones that favour CH_4 production (Covey and Megonigal 2019). This effect might be further intensified during winter when reduced transpiration could lead to even lower O_2 availability within the tree (Machacova et al. 2016). Overall, these findings underscore the complex interplay of environmental and biological factors in driving stem CH_4 emissions and highlight the need for further investigation into the mechanisms behind CH_4 dynamics in reclaimed forest ecosystems.

In contrast, the stem CH_4 emissions were barely linked to atmospheric parameters such as air temperature and relative humidity, as reported by Pangala et al. (2014). These findings, coupled with the decreasing emissions with height (Fig. S2), suggest that the processes governing CH_4 production and release from trees may be more closely tied to soil conditions than to atmospheric temperature and moisture levels, despite the coupling of stem CH_4 emissions and tree physiology influenced by atmospheric parameters (Pitz and Megonigal 2017). However, some studies have noted a weak correlation between stem CH_4 emissions and soil parameters (Machacova et al. 2023; Moldaschl et al. 2021). This could be due to the fact that CH_4 emissions may primarily originate from in-plant CH_4 production rather soil CH_4 production, or it could be attributed to variations influenced by multiple factors.

Species-specific stem CH_4 emissions

Environmental conditions were similar for *Populus euramericana*, *Metasequoia glyptostroboides*, and *Camphora officinarum* (Fig. 6), yet their stem CH_4 emissions varied significantly, suggesting that plant traits might affect the emissions. This finding aligns with studies in nature forest ecosystems where species-specific stem emissions were attributed to various plant-related factors, e.g., gas transport mechanisms, DBH, wood and lenticel density, presence of aerenchyma and pneumatophore, CH_4 production and oxidation inside plants, as well as photosynthesis and transpiration (Barba et al. 2019; Covey and Megonigal 2019; Moisan et al. 2024; Putkinen et al. 2021).

In this study, *P. euramericana* exhibited the highest stem emissions among the investigated species, likely due to favourable traits: (i) the extensive roots that penetrate CH_4-rich layers (Stettler 1996), enhancing CH_4 absorption; (ii) the low wood density (Table 2), and the vessels with high diffusivity facilitating gas movement (Cochard et al. 2001; Rodriguez and Luquez 2016); and (iii) the high lenticel density (Table 2) offering less resistance for gas to diffuse from the stem to the atmosphere. Furthermore,

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CH_4 production within the stem of *P. euramericana* may occur, supported by the detection of methanogens in the stem of *Populus* (Feng et al. 2022; Moisan et al. 2024). *Populus* is often planted in reclaimed forests (Wu and Wang 2016) due to its fast growth, high vegetative reproduction, and adaptability to diverse environmental conditions (Ceulemans and Deraedt 1999; Stettler 1996). The high emissions observed in our study imply that sites dominated by this tree could potentially be significant CH_4 emission hotspots. In contrast, *C. officinarum* showed the lowest CH_4 emissions. This species belongs to hardwoods and thus possesses a complex vascular system comprising vessels and fibres that facilitate the transport of water, nutrients, and gas throughout the plant (Lucas et al. 2013; Wiedenhoeft and Miller 2005). However, the gas transport could be restrained by the small lenticel density and high wood density (Table 2).

The stem CH_4 emissions from *M. glyptostroboides* were higher than those from *C. officinarum*, despite the former being classified as a softwood and having a fibrous and shallow root system (Williams 2005), potentially limiting its penetration into deep, CH_4-rich soils. Gas transport and diffusion may benefit from the low wood density (Table 2), as found in previous studies (Barba et al., 2019; Pangala et al. 2023; Wu et al. 2024). The smaller DBH of *C. officinarum* might also enhance stem CH_4 emissions by reducing diffusion paths, similar to findings reported by Pangala et al. (2013). However, DHB has been found to positively affect stem CH_4 emissions (Pitz et al. 2018). This inconsistency might result from the complex interactions between tree size, microbial processes, and physiological adaptations affecting CH_4 dynamics in trees. Therefore, measurements should carefully consider variables such as sample size, diameter range, stem age, species, and ecosystem type to account for potential confounding factors and ensure accurate assessment of CH_4 emissions.

The contribution of tree-mediated CH_4 emissions

Our results highlight that significant CH_4 emissions come from soil, trees, and herbaceous plants (Fig. 7, Table 3). Soils act as both sources and sinks of CH_4, with methanogens producing CH_4 under anaerobic conditions and methanotrophs consuming it under aerobic conditions (Feng et al. 2020; Guo et al. 2023). Trees emit CH_4 through internal transport mechanisms, where soil-produced CH_4 diffuses into the roots and is emitted via the stem and leaves (Moisan et al. 2024). Herbaceous plants, particularly those with aerenchyma tissues, transport CH_4 directly from the soil to the atmosphere, bypassing soil oxidation processes (Ge et al. 2024a). This distribution could be influenced by factors such as soil

moisture, temperature, organic matter content, and plant physiological processes (Chen et al. 2024; Ge et al. 2024b; Zhang et al. 2022). Understanding these interactions is crucial for accurately assessing the contributions of each component to overall CH_4 flux in reclaimed forests.

Trees made the highest contributions to ecosystem CH_4 flux during spring and winter (Fig. 7, Table 3), consistent with findings in natural forests (Pangala et al. 2015). In spring, the high contribution could be ascribed to the increasing root activity and high porewater CH_4 concentration (Fig. 5), resulting from winter accumulation, increased soil moisture, and temperature. By contrast, although the shoots of herbs started to emerge in spring, the low amounts of new roots and poorly developed aerenchyma might restrict gas transport and diffusion in the soil-herb-atmosphere continuum (Fagerstedt, 1992; Hultgren, 1989). Similarly, trees contributed more to ecosystem CH_4 flux than herbs did in winter because tree roots might still be active even during dormancy in temperate zones (Malyshev et al. 2023), whereas both the roots and shoots of herbs were expected to deteriorate and collapse.

However, herbs surpassed trees in contributing to ecosystem CH_4 flux during summer, due to their fully grown and highly permeable roots and the well-developed aerenchyma (Bernard and Fiala 1986; Fagerstedt 1992). Similar to our results, previous studies have reported that herbs could mediate highest proportion of ecosystem CH_4 during periods of rapid growth (Whiting and Chanton 1992). The contribution of herb-mediated CH_4 emissions dropped significantly in autumn (Fig. 7, Table 3) when the herbs were in senescence (Kim et al. 2018; Kositsup et al. 2010; Nouchi et al. 1990; Ström et al. 2003). Our results match previous studies highlighting the important role of growing stage in regulating CH_4 emissions from herbs (Ge et al. 2023, 2024b). Take together, our results suggest that the primarily source of CH_4 to the atmosphere can shift with seasons, which have implications for CH_4 budgets, climate change feedbacks, and ecosystem functioning.

The limitations of this study

This is the first study that investigated the magnitude, seasonality, drivers, and contributions of tree-mediated CH_4 emissions in reclaimed forests with different reclamation period. However, some limitation and uncertainties in this study should be acknowledged. We could not fully elucidate the CH_4 emission pathways from tree stems because we did not conduct stable isotope analysis, which effectively traces CH_4 origins (Whiticar 1999), nor microbial analysis, which reveals the presence of methanogens (Lenhart et al. 2012). Additionally, while

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measuring CH_4 fluxes at multiple soil depths and distances from trees can help distinguish the sources of stem CH_4 emissions, we only measured CH_4 flux from the surface soil. Future research incorporating these methods are needed to provide a more comprehensive understanding of CH_4 emission sources in reclaimed forests. Besides, we did not measure CH_4 flux from branches and leaves, two potential sources of atmospheric CH_4 (Ernst et al. 2022; Keppler et al. 2006; Tenhovirta et al. 2022; Wang et al. 2011). This omission hinders our ability to construct models that could accurately estimate ecosystem CH_4 flux. Furthermore, we did not conduct soil property analysis, so we cannot confirm how did reclamation affected tree CH_4 emissions through influencing soil properties; future work is needed to reveal the precise mechanism. Lastly, our results may be biased by the discontinuous measurements. To precisely identify the dynamics of tree-mediated CH_4 emissions, long-term and continuous measurements are necessary.

Conclusion

While our study indicates that trees in reclaimed forests can emit significant CH_4, it is essential to acknowledge that previous studies predominantly report forests as CH_4 sinks due to substantial CH_4 oxidation by soils (Feng et al. 2023; Wu et al. 2020; Zhou et al. 2021a; Zhou et al. 2021b). Future research should integrate both tree and soil CH_4 flux measurements to better understand the overall CH_4 budget of forests. Our study showed that the length of the reclamation period could significantly impact stem CH_4 emissions, with older, more mature reclaimed forests potentially becoming substantial CH_4 sources on regional and global scales once they achieve sufficient ecological restoration. We also found that the stem CH_4 emissions varied seasonally, influenced by changes in tree phenology as well as soil parameters, including soil CH_4 flux, porewater CH_4 concentration, and soil temperature and water content. Given the species-specific nature of stem CH_4 emissions, more trees should be investigated, and plant trait analyses are necessary to identify suitable proxies for predicting ecosystem-scale emissions. Additionally, we found that the primary sources of atmospheric CH_4 in reclaimed forests shift seasonally, which should be considered in predicting ecosystem CH_4 emissions. These findings underscore the importance of integrating seasonal dynamics and forest age into ecosystem CH_4 models. Improved modelling accuracy will enhance our ability to predict greenhouse gas emissions and inform effective reforestation and climate change mitigation strategies.

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