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RESEARCH ARTICLE

Morphological constraints on plant-mediated methane release and oxidation under experimental warming in a peatland and meadow on the Qinghai-Tibetan Plateau

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Abstract

1. Alpine meadows and peatlands on the Qinghai-Tibetan Plateau, respectively, act as sinks and sources of atmospheric CH_4. Yet, little is known about plant-mediated CH_4 fluxes in these ecosystems.
2. We measured CH_4 flux from shoots of plants in both ecosystems (45 and 7 species, respectively) and investigated its response to experimental warming. We further investigated the CH_4 transport mechanism of key plant species in the peatland through shading and clipping experiments and scanning electron microscope analysis.
3. In the meadow, most plant families showed negative plant CH_4 flux (CH_4 uptake), ranging from −0.0005 to −0.04 mg CH_4 g^{-1} g h^{-1}. The plant CH_4 flux in the peatland was positive for all species but showed large between-species variation, ranging from 0.0006 to 0.167 mg CH_4 g^{-1} g h^{-1}. Experimental warming did not affect plant CH_4 flux in the peatland, while it negatively affected CH_4 uptake in the meadow. Plant CH_4 transport mechanisms in the peatland were species-specific: the dense exodermes of the primary roots restrained transport in *Blysmus sinocompressus* and *Carex myosuroides*, while leaves controlled transport in *Carex muliensis* due to small aerenchyma and limited connectivity.
4. Our findings have important implications for the regional CH_4 budget and show that species-level differences should be considered when assessing plant-mediated CH_4 emissions.

KEYWORDS
CH_4 transport mechanisms, experimental warming, plant-mediated CH_4 fluxes, Qinghai-Tibetan Plateau, shading and clipping experiments

1 | INTRODUCTION

Methane (CH_4) is a powerful greenhouse gas with a global warming potential over 30 times greater than carbon dioxide over a 100-year period (Saunois et al., 2020). Since 1750, CH_4 has contributed approximately 20% to global warming, making it a significant driver of climate change (Forster et al., 2021). Wetlands are the largest and increasing natural source of CH_4 (Zhang et al., 2023), where ecosystem emissions can be significantly enhanced by plant-mediated CH_4 transport, which is an efficient pathway for soil-produced CH_4 to escape into the atmosphere, bypassing oxidation in oxic surface soils (Findlay, 2020). Aerenchymous plants have specialized tissues for gas transport, making them especially efficient in CH_4 transport to the atmosphere (Dise, 1993; Noyce et al., 2014). Paradoxically, plants may also act as net sinks of atmospheric CH_4, particularly in well-drained, oxic soils where methanotrophic activity dominates (Cao et al., 2008). This net uptake results from two key mechanisms: (1) internal CH_4 oxidation by methanotrophic microbes inhabiting plant tissues (Raghoebarsing et al., 2005), and (2) oxygen transport to methane-oxidizing bacteria in the rhizosphere (Carmichael et al., 2014). These processes collectively enable plants to mitigate atmospheric CH_4, especially in ecosystems such as alpine meadows (Lin et al., 2015).

The net effect of plant-mediated CH_4 fluxes varies dramatically across ecosystems. Globally, northern peatlands dominate natural CH_4 emissions (~30% of total fluxes), where waterlogged conditions favour plant-mediated transport (Masson-Delmotte et al., 2021). In contrast, well-drained alpine meadows typically function as net CH_4 sinks due to oxygen-enhanced methanotrophy (Qin et al., 2023; Wang et al., 2022). The Qinghai-Tibetan Plateau (QTP) presents a unique study system, encompassing both extensive peatlands (e.g. Zoige Plateau) and alpine meadows. Notably, the QTP has experienced intense warming at 0.3°C per decade—approximately twice the global average rate (Bhattacharya et al., 2021; Kraaijenbrink et al., 2021). Warming may alter plant-mediated CH_4 dynamics through multiple interconnected pathways, including modifications to plant physiology (e.g. stomatal conductance, aerenchyma connectivity) (Crous, 2019; Crous et al., 2022; Evans, 2004; Sadok et al., 2021) and microbial metabolic processes governing net CH_4 production/consumption (Ge et al., 2023; Putkinen et al., 2021).

Consequently, these biological processes may create either positive or negative feedbacks to climate warming by respectively enhancing or reducing CH_4 emissions. While the QTP's exceptional warming rate makes it a critical region for studying these feedbacks, quantitative assessments of vegetation's role in the CH_4 balance of its contrasting ecosystems are lacking. Plant-mediated CH_4 transport and its temperature sensitivity remain unknown, severely limiting our ability to predict future climate–ecosystem interactions. The mechanisms controlling plant-mediated CH_4 transport also remain unresolved in the QTP and beyond. While some studies suggest that leaves and stomata control CH_4 release from plants (Morrissey et al., 1993; Schimel, 1995), other studies suggest that most CH_4 can be emitted from micropores or cracks on stems or leaf sheaths (Nouchi et al., 1990; Shannon et al., 1996). Additionally, below-ground tissues and organs (rhizosphere-root or root–shoot interface) may actually be the rate-limiting step for CH_4 transport, with root removal significantly reducing CH_4 flux compared to minimal effects from leaf excision (Henneberg et al., 2012; MacDonald et al., 1998). These discrepancies likely reflect species-specific adaptations and methodological differences, underscoring the need to resolve mechanistic uncertainties for accurately scaling plant-level CH_4 transport to ecosystem budgets in the QTP's vulnerable ecosystems.

In this study, we measured CH_4 flux from the shoots of common plants in an alpine meadow and a peatland (45 and 7 species, respectively), two ecosystems that are critical for the regional CH_4 budget and climate feedback on the QTP. We used the plant-enclosure technique that allows us to observe plant CH_4 flux from the shoots of plants without disturbing the below-ground organs and tissues (Dorodnikov et al., 2011; Ge et al., 2023). To investigate the response of plant CH_4 flux to climate warming, we measured CH_4 flux under ambient conditions and under experimental above-ground and below-ground warming in the field. To identify which parts of the dominant plants control CH_4 transport in the peatland, where we expected to see the highest fluxes, we combined scanning electron microscopy (SEM) to examine the structure of roots and leaves, and plant manipulation experiments, including prolonged darkness and leaf clipping and sealing. We hypothesized that plants in the alpine meadow can cause CH_4 oxidation (negative flux), while peatland plants would act as conduits of soil-produced CH_4 to the atmosphere (positive flux); the experimental warming could affect plant CH_4 fluxes in both ecosystem types; and CH_4 transport mechanisms may vary between plant species in the peatland due to species-specific traits.

2 | MATERIALS AND METHODS

2.1 | Site description

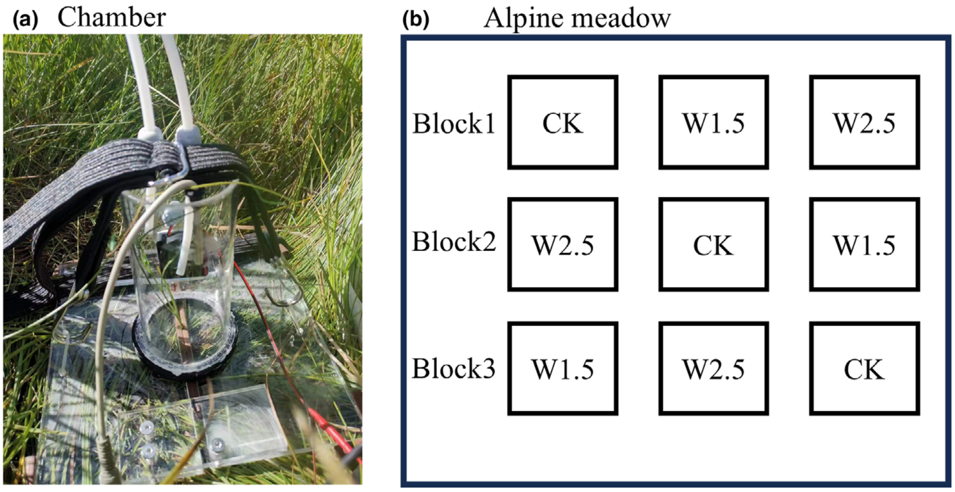
The study sites, an alpine meadow and the Zoige peatland, were situated in Hongyuan County, Sichuan Province (32°58′ N, 102°37′ E; 3475 m a.s.l.), on the northeastern margin of the QTP. The distance between these two measurement sites was around 37 km. The annual mean (1961–2015) temperature and precipitation in Hongyuan County were 1.57°C and 752 mm, respectively (Chinese Meteorological Data Service Centre, http://data.cma.cn//). The mean temperature of the coldest month, January, was −9.66°C and of the warmest month, July, was 11.12°C, respectively.

These sites represent two contrasting ecosystem types typical of the QTP: a typical alpine meadow and a sedge-dominated peatland. The alpine meadow featured well-drained soils, with the water-table consistently deeper than 50 cm, a soil pH of 6.2 ± 0.3 and a soil organic carbon (SOC) content of 5.8 ± 0.7%. In contrast, the peatland was permanently water-saturated, with a shallow water-table depth of 10–20 cm below the surface, a pH of 6.0 ± 0.2 and a substantially higher SOC content ranging from 35% to 40%. Both sites exhibited homogeneous vegetation composition and showed no signs of recent human disturbance. The typical plant species in the meadow included forbs (*Anemone rivularis*, *Artemisia roxburghiana*, *Potentilla anserina*, *Artemisia roxburghiana*, *Taraxacum* spp. and *Pedicularis verticillata*), grasses (*Deschampsia caespitosa* and *Elymus nutans*), sedges (*Blysmus sinocompressus*, *Carex enervis* and *Carex muliensis*) and the shrub *Salix cupularis*. In the peatland, sedges (*Carex muliensis*, *Carex myosuroides* and *Blysmus sinocompressus*) were the most dominant species, with some forbs (*Potentilla anserina*, *Leontopodium leontopodioides*, *Sanguisorba filiformis* and *Caltha scaposa*) also present.

2.2 | CH_4 flux measurements

The experiments were conducted during peak growing season (July–August 2023) to avoid phenological effects, consistent with the previous study (Ge et al., 2023). The sampling was further restricted to 8:00 AM–5:00 PM local time to minimize diurnal CH_4 flux variations (Ding et al., 2005). All measurements were conducted on mature, fully expanded leaves within homogeneous vegetation blocks to minimize developmental stage variations. The experimental setups in the meadow and peatland included: (1) baseline CH_4 flux measurements that measured CH_4 flux from the shoots of 45 and 7 plant species (Table S1) in the alpine meadow and peatland, respectively (Experiment I); (2) multi-level warming treatments to reveal the effects of experimental warming on plant CH_4 flux (Experiment II); (3) shading and clipping experiments to reveal CH_4 transport mechanisms of the common sedges *B. sinocompressus*, *C. muliensis* and *C. myosuroides* in the peatland (Experiment III). For the details of these three experiments, see the following sections.

We measured CH_4 fluxes from the entire shoots of the plants that represented the common species in the meadow and peatland (Figure 1a). We used the chamber system developed by Korrensalo et al. (2021), which consisted of two plexiglass plates and a transparent polymethyl methacrylate chamber (volume 0.0006 m^3). The shoots were separated from the soil by two plexiglass plates attached around the lower part of the stem. During each measurement, we put the transparent chamber on top of the plates to cover the shoots. To ensure the airtightness of the system, we pressed the chamber towards the plates with rubber bands attached to the edges of the plates and put a smooth rubber seal between the plates and the bottom of the chamber. The chamber system had



(c) Zoige peatland

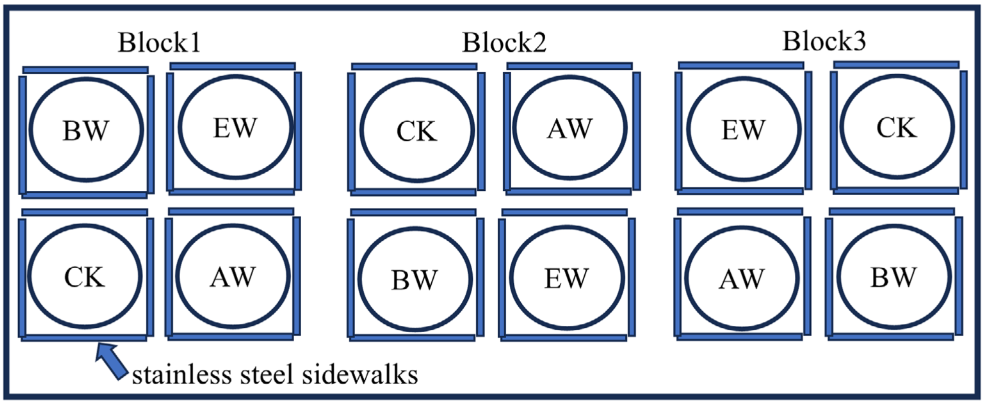


FIGURE 1 Plant-mediated CH_4 flux measurement chamber (a) and the layout of the manipulative warming experiments in the alpine meadow (b) and Zoige peatland (c).

a 12 V electric fan to mix the headspace air inside the chamber. During the measurements, the headspace gas was circulated between the closed chamber and the analyser (Los Gatos Research LGR-UGGA). In Experiments I and II, each chamber closure lasted for 5 min. In Experiment III, the shading treatment comprised an initial 5-min flux measurement under light conditions followed by 90 min of continuous observations after darkening, while the clipping treatment involved a series of 5-min chamber closures under sequential experimental conditions. CH_4 fluxes were calculated as the linear change of CH_4 concentration over the closure time (dC/dt, Equation 1).

$$F = \frac{dC}{dt} \times \frac{MPV}{RT\,m} \times 3600, \tag{1}$$

where F is CH_4 flux (mg CH_4 g^{-1} shoot dry biomass h^{-1}), M is the molar mass of CH_4 (16,042 mg), P is atmospheric pressure (66,560 Pa), V is chamber volume (m^3), R is gas constant (8.3144598 J K^{-1} mol^{-1}), T is chamber temperature (K) and m is dry biomass of the shoot enclosed in the chamber.

After each flux measurement event, we measured the leaf area (sedges in the peatland only) and dry biomass enclosed in the chamber. The single-sided leaf area of the sedges was measured by digital scanner and the IMAGJ program (Ferreira & Rasband, 2012). We measured dry biomass by drying the shoots at 60°C for 24 h. Using the dry biomass data, plant CH_4 flux (mg CH_4 g^{-1} dry biomass h^{-1}) was estimated by dividing CH_4 flux by the dry biomass enclosed in the chamber.

2.3 | Experiment I: Investigation of plant CH_4 flux

We investigated plant-mediated CH_4 fluxes in both alpine meadow and peatland ecosystems. Peatland measurements were conducted from 1 to 7 July across three vegetation blocks (2 × 2 m, <5 m interblock spacing), all representing a similar type of homogeneous vegetation characterized by an intermediate lawn community. We focused on seven ecologically significant species, including three dominant sedges (*Blysmus sinocompressus*, *Carex muliensis* and *C. myosuroides*) and four characteristic forbs (*Sanguisorba filiformis*, *Caltha scaposa*, *Leontopodium alpinum* and *Potentilla anserina*).

Subsequently, meadow surveys were conducted from 8 to 19 July across nine sampling blocks, designed to capture the higher biodiversity of the site. Each block comprised three spatially separated subblocks (2 × 2 m, spaced approximately 3 m apart), with all measurements taken more than 1 m from pathways to reduce edge effects. Each of the 45 target species was measured in three different subblocks ($n = 3$ replicates per species), with each replicate monitored 3–4 times per day. As the vegetation composition varied, each subblock typically contained multiple species for measurement (see full species list in Table S1). This sampling strategy ensured: (1) representative inclusion of dominant and co-occurring species, (2) sufficient spatial independence among replicates and (3) minimal disturbance during flux measurements.

2.4 | Experiment II: Experimental warming

To investigate the response of plant CH_4 fluxes to climate warming, we conducted flux measurements within established warming experiments (Figure 1a,b) in both peatland and meadow ecosystems between 22 July and 10 August 2023. In the peatland, the studied species comprised the three sedges (*B. sinocompressus*, *C. myosuroides* and *C. muliensis*) and four forbs (*P. anserina*, *S. filiformis*, *C. scaposa* and *L. alpinum*) examined in Experiment I. In the meadow, one sedge (*C. enervis*), one grass (*E. nutans*) and two forbs (*A. rivularis* and *Artemisia roxburghiana*) were investigated. All selected species were present in every subblock across the experimental blocks at both sites. For each species, we measured three replicates per treatment ($n = 3$), corresponding to the three replicate blocks. Each replicate was measured three to four times per day.

In the peatland, the warming experiment had been started 1 year before measurements in a randomized complete block design with three replicate blocks (Figure 1c) with vegetation showing complete recovery from installation disturbance by the study period. The experiment targeted different components of the warming process by having within each block four 2 m diameter subblocks randomly assigned to (1) ambient control (CK), (2) above-ground warming (AW) to represent increased solar radiation, (3) below-ground warming (BW) to mimic deeper soil heat flux and (4) combined warming (EW) to assess the response to both above- and below-ground warming. For AW, MSR-2420 infrared heaters (Kalglo Electronics; 165 × 15 cm; 240 V AC) were suspended 1.5 m above ground and due to wind effects, AW only increased soil temperature at 5 cm depth by <2°C. BW was implemented using GX-088L3100 heating cables (Danfoss; 9.8 Ω m^{-1}) installed vertically to 1 m depth in a 15 × 15 cm grid pattern, yielding a 1.7 to 3.1°C soil warming. The EW treatment that combined both systems resulted in a 1.7 to 5.9°C soil warming. To simulate the shading effect of the infrared heaters in CK, we also suspended a ‘dummy’ heater with the same size and shape as the infrared heater 1.5 m above each control subblock.

The meadow experiment had been established 10 years prior to this study and followed a similar randomized block design as in the peatland but focused on AW only with three levels of warming: a control (CK), low-level warming (+1.5°C, LW) and high-level warming (+2.5°C, HW) to simulate different warming scenarios. There were three blocks and within each block (Figure 1b), three sub-blocks (3 × 2 m), each with one warming level. Using the same infrared heater model mentioned above, we adjusted power outputs to 1000 W (LW) and 2000 W (HW). The mean soil temperature under CK, LW and HW was 12.4°C, 13.9°C and 14.3°C, respectively.

2.5 | Experiment III: Mechanisms of plant CH_4 transport and release

2.5.1 | Shading and clipping experiment

The shading experiment was conducted from 12 to 19 August 2023 to investigate the role of stomatal regulation in CH_4 emissions from the three sedges *B. sinocompressus*, *C. muliensis* and *C. myosuroides*. For each species, one specimen was selected. We first measured CH_4 flux for 5 min under ambient light conditions using a transparent chamber. Immediately afterwards, the chamber was covered with an opaque enclosure to simultaneously impose darkness and allow CO_2 accumulation, thereby inducing stomatal closure. CH_4 flux was then monitored continuously for 95 min under these conditions.

After the shading experiment, we selected three new replicates for the same three species for a clipping experiment. All measurements were conducted using transparent chambers with a 5-min closure time. For all species and replicates, we first measured the baseline CH_4 flux from intact shoots under ambient conditions (CK). With *B. sinocompressus*, the clipping treatment included the removal of the leaf blades with intact stem (Clipping only) to investigate the resistance of leaf blades to CH_4 transport, and secondly, sealing the cut surfaces of the remaining stem with silica gel (Clipping + Sealing) to investigate the amount of CH_4 released from the stem. As for *C. muliensis* and *C. myosuroides*, we clipped the plants 4 cm above the soil surface (Clipping only). Due to the morphological structure of these species—where aboveground biomass consists mainly of leaf blades with minimal stem tissue—the material remaining after clipping was primarily composed of leaf bases and sheaths, lacking a distinct stem structure suitable for sealing. Therefore, the 'Clipping + Sealing' treatment was not conducted for these species.

2.5.2 | Scanning electron microscope analysis

Scanning electron microscopy was used to analyse the aerenchyma structure in the three dominant sedge species of the peatland—*B. sinocompressus*, *C. muliensis* and *C. myosuroides*. The study specifically aimed to characterize aerenchyma type, spatial organization and its anatomical association with surrounding root tissues. The first step was to dehumidify all specimens in an ascending ethanol sequence (30%, 50%, 70%, 80%, 90%, 95% and 100%) and dried in a critical point dryer (Autosamdri-931, Tousimis, Maryland, USA). Then, the leaf blades and the cross-sections of the primary and fine roots of the aforementioned species were dissected with sterile razor blades. Finally, we evenly deposited a 50 nm thick gold film on the sample pieces, which were then examined with a scanning electron microscope (Zeiss Sigma 300, Oberkochen, Germany).

2.6 | Statistical analyses

Prior to analysis, the datasets were inspected for outliers using boxplots. Normality was assessed using Shapiro–Wilk tests, and log transformations were applied when necessary. Homogeneity of variances was verified using Levene's test. All analyses were conducted in R version 3.6.1 (R Core Team, 2019).

To examine potential differences in plant-mediated CH_4 fluxes, we applied a one-way ANOVA followed by Tukey's HSD test (Experiments I). In the alpine meadow, ANOVA analyses were conducted at the plant family level due to the high species diversity and the functional consistency of CH_4 transport within families, which allows for more ecologically meaningful grouping. In the peatland, where a few sedge species dominated, the analysis was performed at the species level.

To evaluate the effects of experimental warming and clipping on plant CH_4 flux, we used linear mixed-effects models (LMMs) with Tukey's HSD post hoc comparisons (Experiments II and III). The LMMs were performed separately for each species in both ecosystems. In Experiment II, nested random effects of block and sample ID (block/sample ID) were included to account for non-independence among repeated measurements from the same plant and among plants within the same block. Warming treatment was specified as a fixed effect, with different levels for meadow (CK, LW and HW) and peatland (CK, AW, BW and EW). For Experiment III, the same plant received sequential treatments (intact, clipping only and clipping with sealing), so sample ID was included as a random effect to model repeated measures. Clipping treatment was treated as a fixed effect in separate models for each stage.

3 | RESULTS

3.1 | Plant CH_4 fluxes of common plants in the alpine meadow and Zoige peatland

In the meadow, plant CH_4 flux varied significantly among plant families ($p < 0.001$, Figure 2a), based on three replicates per species, with 45 species in total. Most families showed an uptake of CH_4, the plant CH_4 flux ranging from −0.04 to 0.002 $mg\,g^{-1}\,h^{-1}$. *Lamiaceae* showed the smallest plant CH_4 flux, that is, the highest uptake, with a mean of −0.04 $mg\,g^{-1}\,h^{-1}$. The second smallest plant CH_4 flux was found in *Poaceae* and *Rosaceae*, with a mean of −0.02 $mg\,g^{-1}\,h^{-1}$ for both. The other families showed smaller CH_4 uptake or emission, with *Euphorbiaceae* exhibiting the highest plant CH_4 flux with a mean emission of 0.002 $mg\,g^{-1}\,h^{-1}$.

In the peatland, the plant CH_4 flux varied between plant species ($p < 0.001$, Figure 2b). All species emitted CH_4, *Blysmus sinocompressus* exhibiting the highest CH_4 flux (mean: 0.0167 $mg\,g^{-1}\,h^{-1}$), which was significantly greater than that of all other species ($p < 0.001$). Among these, the mean fluxes of *Carex myosuroides* and *C. muliensis* (both 0.0029 $mg\,g^{-1}\,h^{-1}$) were approximately five times higher than that of *Caltha scaposa*, which showed the lowest emission (0.0006 $mg\,g^{-1}\,h^{-1}$), although these differences were not statistically significant.

3.2 | The effects of experimental warming on plant CH_4 flux

In the peatland, experimental warming did not significantly affect the plant CH_4 flux of any of the studied sedge and forb species (Figure 3;

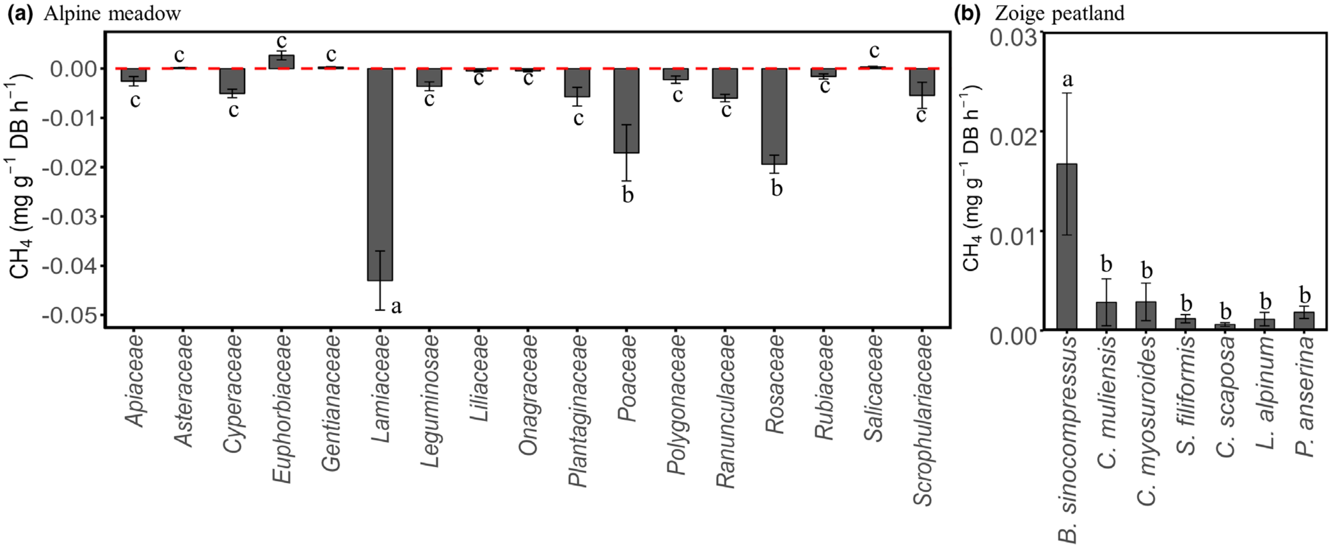


FIGURE 2 Plant CH$_4$ flux (mg CH$_4$ g^{-1} dry biomass h^{-1}) of the common plant families in the alpine meadow (a), and the common sedges and forbs in the Zoige peatland (b) on the Qinghai-Tibetan Plateau. Error bars represent standard deviation. Letters above bars denote significant differences ($p < 0.05$) between plant families (meadow) and species (peatland).

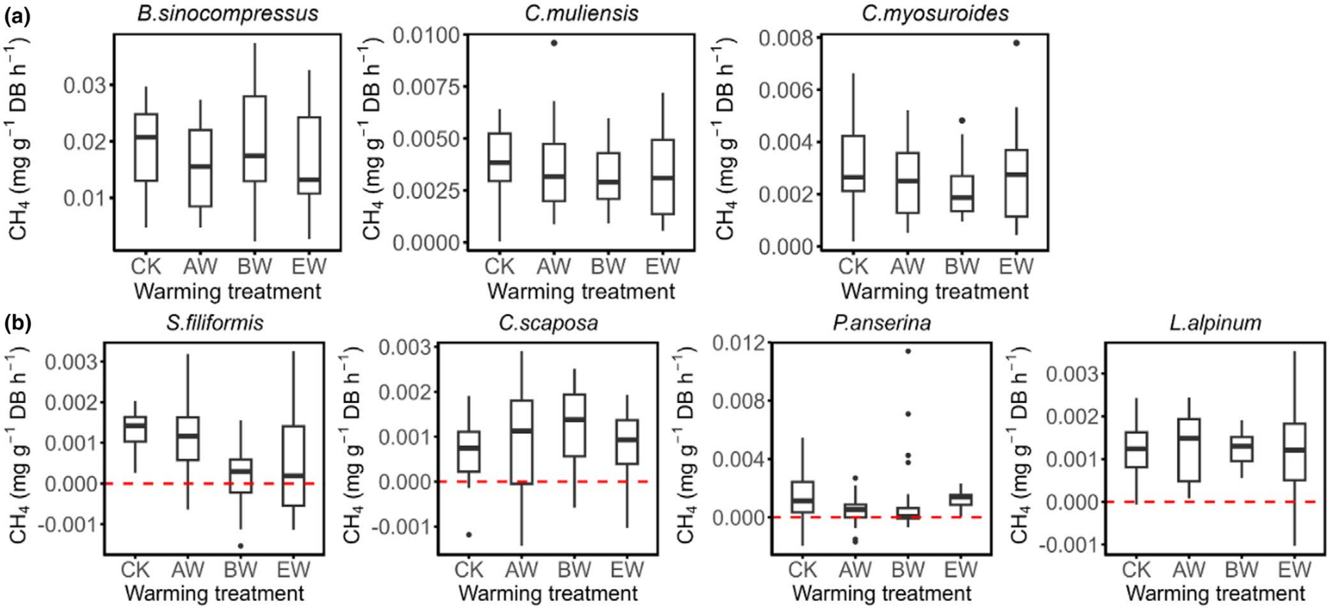


FIGURE 3 The effects of experimental warming on plant CH$_4$ flux (mg CH$_4$ g^{-1} dry biomass h^{-1}) of plant species belonging to sedges (a) and forbs (b) in the Zoige peatland. Experimental warming included control (CK), above-ground warming (AW), below-ground warming (BW) and entire warming (EW, including both above-ground and below-ground warming). Red dashed horizontal line in panels with negative plant CH$_4$ flux denotes zero flux level.

Table S2). In contrast, experimental warming significantly increased plant CH$_4$ flux of all investigated species in the meadow (Figure 4; $p < 0.001$; Table S3), that is, decreased their CH$_4$ uptake. While the plant CH$_4$ flux of *Carex enervis*, *Anemone rivularis* and *Artemisia roxburghiana* was similar between the low-level and high-level warming treatments, the high-level warming led to a stronger decrease in CH$_4$ uptake of *Elymus nutans* than the low-level warming did.

3.3 | The effects of shading and clipping treatment on CH$_4$ flux

CH$_4$ flux from all investigated species displayed a decrease in flux after enclosure (Figure 5a). However, they reached a stable minimum flux at different time points: 30 min for *B. sinocompressus* (mean flux thereafter: 0.00000008 mg g^{-1} h^{-1}), 40 min for *C. myosuroides* (mean

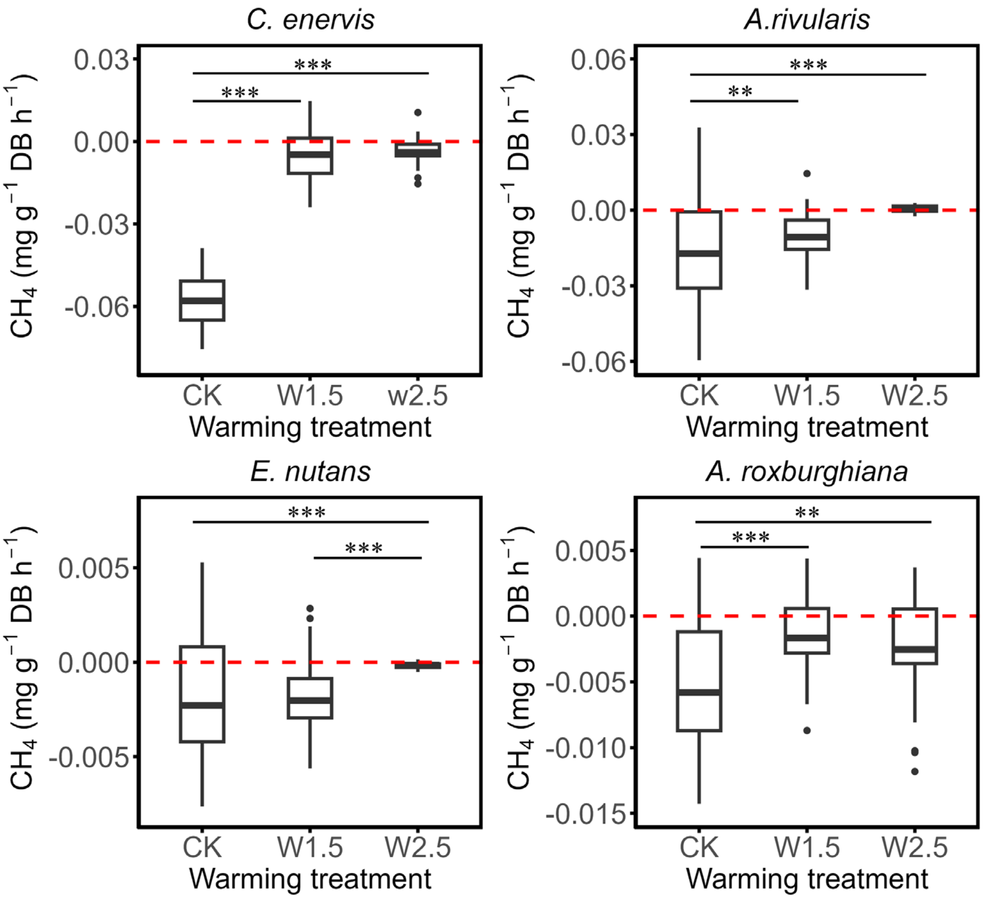


FIGURE 4 The effects of experimental warming on plant CH_4 flux (mg CH_4 g^{-1} dry biomass h^{-1}) of *C. enervis*, *A. rivularis*, *E. nutans* and *A. roxburghiana* in the alpine meadow. Experimental warming includes control (CK), low-level warming (+1.5°C, LW) and high-level warming (+2.5°C, HW). Red dashed horizontal line in panels with negative plant CH_4 flux denotes zero flux level. Asterisks denote statistical significance: **, 0.01, ***, 0.001.

flux thereafter: 0.000000007 mg $g^{-1}h^{-1}$) and only 15 min for *Carex muliensis* (mean flux thereafter: 0.00000005 mg $g^{-1}h^{-1}$). *Carex myosuroides*, which was the highest emitter initially, showed the strongest decrease, with the mean minimum flux being 22 times smaller than that when the enclosure just started.

CH_4 flux from *B. sinocompressus* did not change significantly after clipping leaf blades, but it dropped significantly after clipping leaf blades and sealing the cutting end of the stem (Figure 5b, $p < 0.05$). Similarly, clipping did not affect the CH_4 flux from *C. myosuroides* either. In contrast, the CH_4 flux from *C. muliensis* increased significantly after clipping ($p < 0.05$). Sealing was not done for *C. myosuroides* and *C. muliensis* as their above-ground biomass mainly consisted of leaf blades and no stems were observed. Lastly, CH_4 flux from all intact specimens did not correlate with the leaf area of the investigated species (Figure 5c).

3.4 | Aerenchyma patterns and root traits of the sedges in the Zoige peatland

The scanning electron microscope (SEM) showed that the stomata density was higher in *C. muliensis* and *C. myosuroides* than in *B. sinocompressus* (Figures 6–8). Besides, the aerenchyma type varied between species; for *C. myosuroides*, it even varied between organs. The wheel-shaped schizogeny aerenchyma (i.e. comprising wide air spaces of regular size that were circular or polygonal) was found in the primary root of *B. sinocompressus* (Figure 6b). In contrast, tangential lysigeny aerenchyma (i.e. cell separations and cell collapses occurring in tangential sectors between intact radial files of cells) was observed in the primary root of *C. muliensis* (Figure 8b). As for *C. myosuroides*, it had hollow schizogeny aerenchyma (i.e. characterized by a large cylindrical lacuna in the centre) in the roots (Figure 7b,c), while honeycomb schizogeny aerenchyma (often seen as the intermediate form of wheel-shaped aerenchyma) was observed in the leaf blade (Figure 7d).

Although the aerenchyma in the primary root of *B. sinocompressus* was large, it was separated from the rhizosphere by the dense exodermis (Figure 6e). The exodermis of the fine root of *B. sinocompressus* was much thinner than that of the primary root (Figure 6f). The primary roots of *C. muliensis* and *C. myosuroides* also had a dense exodermis (Figures 7e and 8e), while a thin exodermis was observed in their fine roots (Figures 7f and 8f).

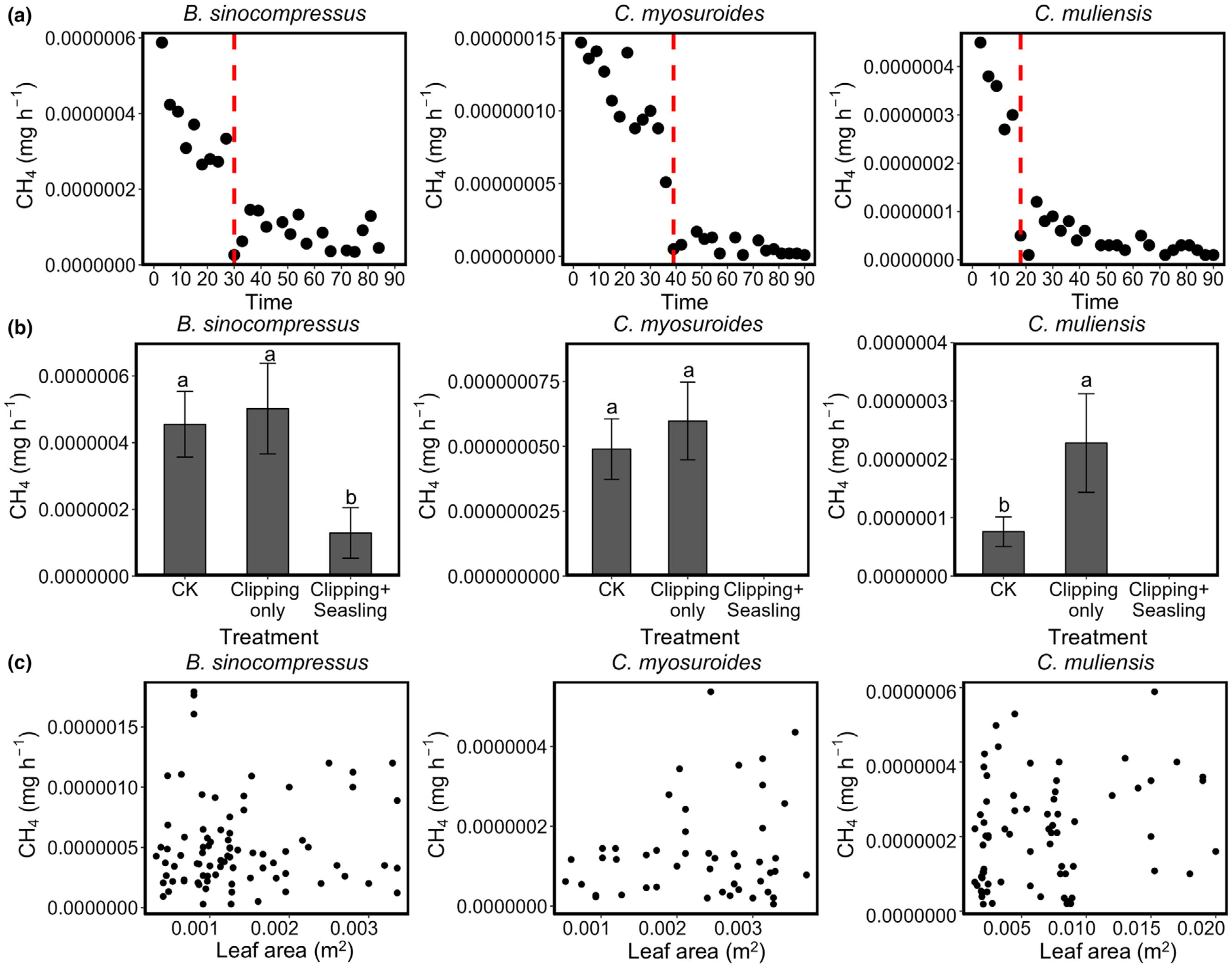
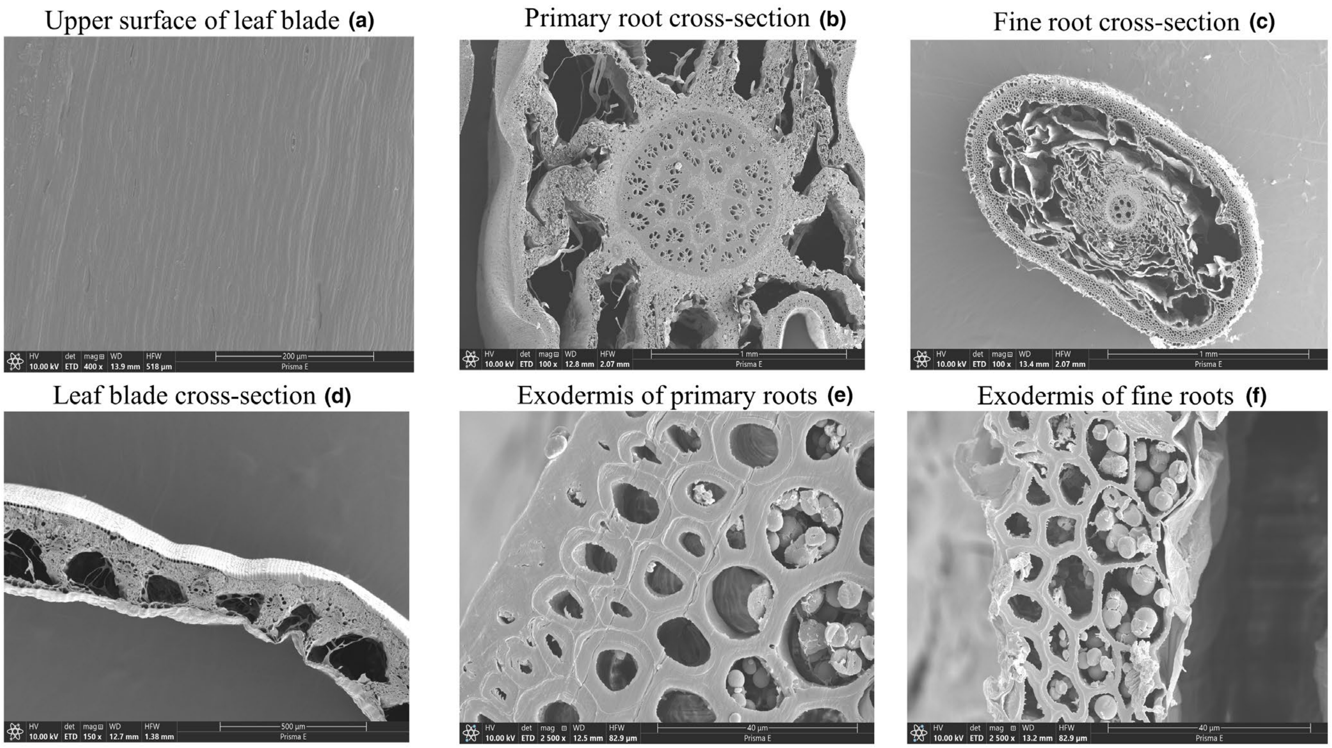


FIGURE 5 CH$_4$ flux (mg h^{-1}) from the shoots of *B. sinocompressus*, *C. myosuroides* and *C. muliensis* over time, (a) following enclosing shoots in the opaque chamber and (b) following clipping of leaf blades and, for *B. sinocompressus*, sealing the stem at 4 cm above the soil surface. (c) The correlation between leaf area and CH$_4$ flux from shoots of *B. sinocompressus*, *C. myosuroides* and *C. muliensis*. Clipping treatments included control (CK), clipping leaf blades but not sealing the stem (Clipping only) and clipping leaf blades and sealing the stem (Clipping and Sealing). No data for the effect of Clipping + Sealing on CH$_4$ flux from *C. myosuroides* and *C. muliensis* due to their lack of stem above the soil surface. Red dashed vertical lines in (a) indicate the time points at which the significant decrease of CH$_4$ flux ended.

4 | DISCUSSION

We examined plant CH$_4$ flux and its response to experimental warming for common plant species in the alpine meadow and peatland on the QTP. Additionally, we examined gas transport mechanisms of three common sedges (*Blysmus sinocompressus*, *Carex muliensis* and *Carex myosuroides*) in the peatland by clipping and shading experiments and investigated their aerenchyma properties with scanning electron microscopy (SEM). To the best of our knowledge, this is the first study where the effects of experimental warming on plant CH$_4$ flux and mechanisms of plant CH$_4$ transport were investigated. It also represents the first comparative assessment of inter-family CH$_4$ flux variation in an alpine meadow and multi-species flux in peatland. Datasets of this comprehensiveness—spanning flux measurements, warming responses and mechanistic traits—are currently unavailable for any other region, despite being critical for developing rigorously parameterized models of current and future ecosystem-scale CH$_4$ emissions.

Consistent with our hypothesis, most plants in the meadow showed negative CH$_4$ flux, while the opposite was true for the peatland plants. We hypothesized that we would find significant effects of experimental warming on plant CH$_4$ flux in both the meadow and peatland. This was only partially supported by our results as warming significantly and negatively affecting CH$_4$ uptake in the meadow, while plant CH$_4$ flux did not respond to warming in the peatland. Further, as hypothesized, the plant CH$_4$ transport mechanism and the plant part limiting CH$_4$ transport were species-specific: CH$_4$ transport of species having dense exodermes in the primary roots, *B. sinocompressus* and *C. myosuroides*, was unaffected by leaf clipping, while *C. muliensis* with small aerenchyma



Upper surface of leaf blade **(a)**

Primary root cross-section **(b)**

Fine root cross-section **(c)**

Leaf blade cross-section **(d)**

Exodermis of primary roots **(e)**

Exodermis of fine roots **(f)**

FIGURE 6 Scanning electron microscope results of the roots and leaf blade of *B. sinocompressus*. Note the different magnification among organs, (a) 400×, (b, c) 100×, (d) 150×, (e, f) 2500×.

and limited connectivity in the leaves had an increased CH_4 flux after clipping of the leaves.

4.1 | Soils are not the single CH_4 sink in the alpine meadow

Previous studies show that oxic soils act as sites of CH_4 oxidation in alpine meadows (Wang et al., 2023; Wu et al., 2020; Zheng et al., 2012). However, the negative plant CH_4 flux of the investigated families in the alpine meadow (Figure 2) implies that plant gas transport also plays a role in regulating CH_4 oxidation. The consistent negative CH_4 fluxes observed across most plant families in our study align with findings from boreal ecosystems (Riutta et al., 2020; Sundqvist et al., 2012) where plants similarly contribute to CH_4 oxidation. While we confirmed the attenuating effects of plants on ecosystem CH_4 flux in the alpine meadow, it remains unclear whether CH_4 oxidation occurred by methanotrophic microbes inside the shoots or roots or whether these plants simply transported CH_4 to the oxic soils.

If the oxidation happens in the soil, the gas transport efficiency may impact the sink magnitude. If it happens inside the plant, both gas transport and internal microbial community composition matter. Microbial analysis should be conducted to reveal whether oxidation in the soil occurs faster in the presence of plants. However, quantifying the oxidation occurring inside the plant is rather difficult, owing to the fact that methanotrophic microbes may not be uniformly distributed (Baltrus, 2020), their activities may vary with changing environments (Nguyen et al., 2021) and current analytical techniques may struggle to quantify the low level CH_4 concentration inside the plants (Putkinen et al., 2021). Even the presence of oxidizing microbes does not decisively prove that the oxidation in the plant is of sufficient magnitude to matter for the whole ecosystem. Nevertheless, our finding shows that at least part of the CH_4 sink of these ecosystems is mediated through plants, and that the CH_4 sink mediated by plants varies among the studied plant families. This result suggests that further studies should address the importance of the differences in plant CH_4 transport in regulating CH_4 oxidation at the ecosystem and regional level.

Some plants in the alpine meadow of this study displayed CH_4 emissions. These plants had very shallow root systems that grew in oxic soils, suggesting that the emitted CH_4 may not mainly originate from the soils. Instead, plant-derived CH_4 could also be the source of the emitted CH_4. Plant compounds such as pectin (Keppler et al., 2006), lignin, cellulose (Vigano et al., 2008) or methionine (Althoff et al., 2014) could be precursors in this process, and the driving force might be the solar radiation, as alpine meadows receive the most sunlight in all of China (Wang & Qiu, 2009). It is also possible that the emitted CH_4 was plant-derived through microbial processes, as methanogens have been found to dwell on many plant species (Ge et al., 2023; Putkinen et al., 2021). However, the emitted CH_4 could also originate from anaerobic microsites within the otherwise oxic soil matrix. Notably, the plant CH_4 flux in our study could be up to 300 times larger than the emission of Scots pine reported by Tenhovirta et al. (2022) who used the same field measurement

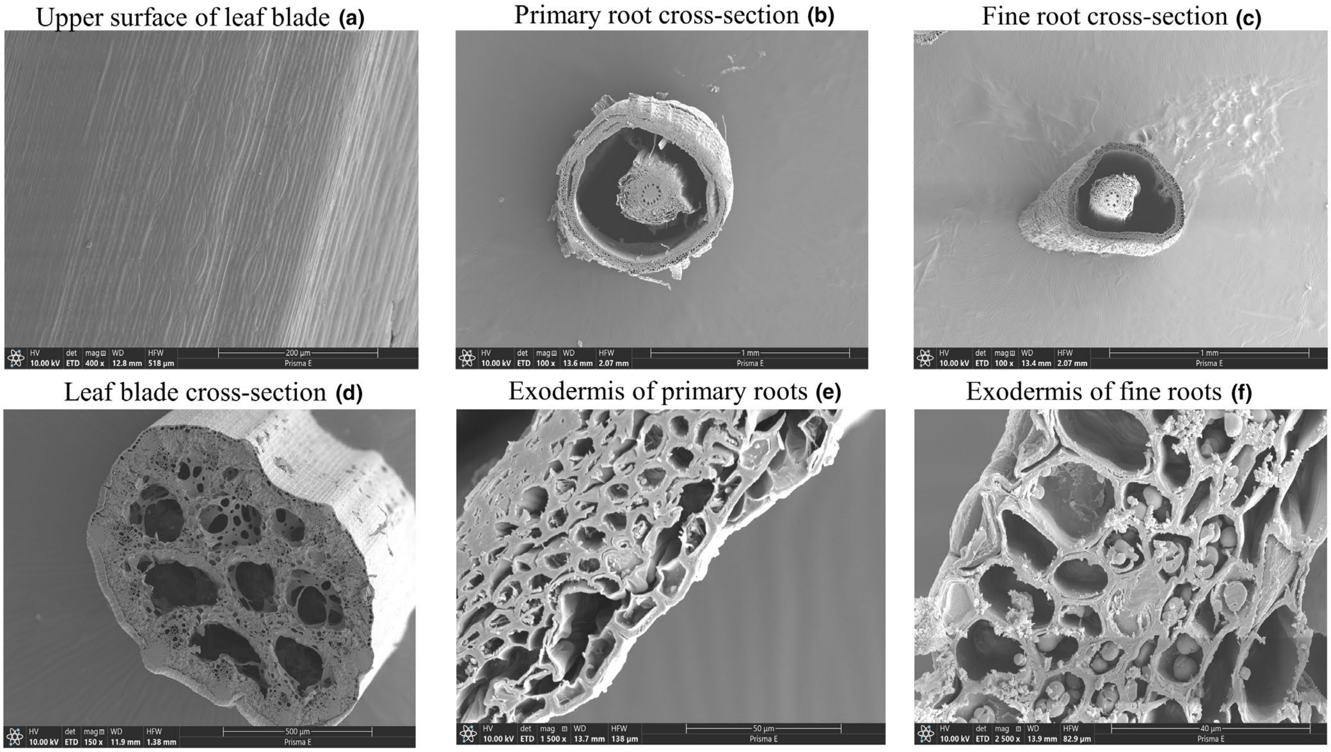

Upper surface of leaf blade **(a)** Primary root cross-section **(b)** Fine root cross-section **(c)** Leaf blade cross-section **(d)** Exodermis of primary roots **(e)** Exodermis of fine roots **(f)**

FIGURE 7 Scanning electron microscope results of the roots and leaf of *C. myosuroides*. Note the different magnification among organs, (a) 400×, (b, c) 100×, (d) 150×, (e, f) 2500×.

method as our study; thus, identifying the sources of the emitted CH_4 is crucial.

4.2 | Different warming effects on plant CH_4 flux in the alpine meadow and peatland

In the alpine meadow, the experimental warming negatively affected CH_4 uptake of all investigated species (Figure 4). The experimental warming has been conducted over 10 years in the site and, thus, the changes in CH_4 uptake could be due to the long-term effects on within-plant and soil microbial communities and bacterial activities (Roldán et al., 2022; Sundqvist et al., 2012; Tveit et al., 2023), as well as changes in plant physiology/morphology. In contrast, Zhang et al. (2021) reported that warming could significantly enhance soil CH_4 uptake in the alpine meadow on the QTP. Together, these results imply that although plant-mediated CH_4 oxidation represents a key pathway for atmospheric CH_4 consumption under ambient conditions, its role may be substantially decreased under sustained warming. This divergent response between plant-mediated and soil-driven CH_4 fluxes highlights the need to incorporate both pathways and their temperature sensitivities into regional CH_4 budget projections.

In contrast, the CH_4 emissions through the dominant sedges and forbs did not respond to any of the warming treatments, and the species-specific differences were retained (Figure 3), suggesting that short-term warming did not directly alter plant-mediated CH_4 transport rate. However, this lack of response should not be interpreted as evidence that warming does not affect peatland CH_4 emissions through other pathways. Indirect effects mediated by changes in soil moisture, microbial community composition and activity could significantly modulate CH_4 production and oxidation and thus, CH_4 availability for plant transport (Peltoniemi et al., 2016; Turetsky et al., 2014). Moreover, vegetation composition may shift under sustained warming—mosses, forbs, sedges and shrubs may respond differently, and the responses further depend on whether warming is accompanied by drying or not (Mäkiranta et al., 2018; Wangchuk et al., 2021). Such shifts could either increase or decrease ecosystem-level CH_4 emissions, largely depending on the fate of sedges that showed the highest plant-mediated flux rates both in this study and more generally in peatland studies (Ge et al., 2023; Korrensalo et al., 2021). The diverse potential trajectories underscore the need for long-term studies integrating vegetation dynamics, soil microbiology and hydrology to elucidate the mechanistic pathways through which warming influences peatland CH_4 emissions.

Poor correlation between plant CH_4 transport rate and soil temperature has also been found in earlier studies on temperate and northern boreal peatlands (Ge et al., 2023; Li et al., 2021). However, Hosono and Nouchi (1997) observed a dependence of the plant CH_4 flux of rice on temperature. The inconsistency might be due to different mechanisms in different plant species, different temperature settings applied in different studies or changes in soil CH_4 concentration with temperature. In laboratory studies like that of Hosono and Nouchi (1997), maximum control of the environment may involve a

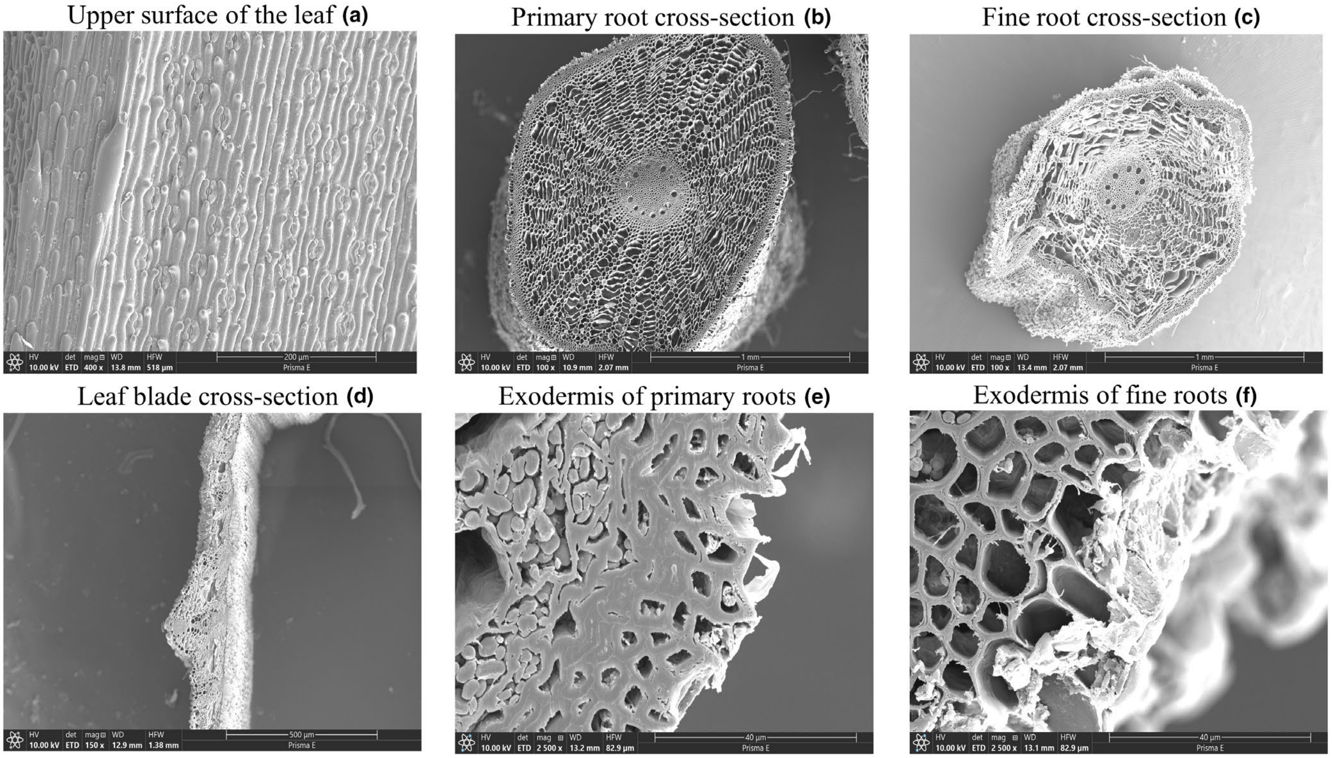


FIGURE 8 Scanning electron microscope results of the roots and leaf of *C. muliensis*. Note the different magnification among organs, (a) 400×, (b, c) 100×, (d) 150×, (e, f) 2500×.

risk of changing plant response. In their study, the low and high-level temperature groups were up to 15°C and 30°C, respectively, and the large temperature difference could alter the physiology of root epidermal layers to transport. In contrast, in our study, the mean soil temperature of all warming treatments increased by less than 3°C, and the measurements were conducted in the field, involving minimal modification of the environment and plant physiology.

4.3 | Species-specific mechanisms controlling plant CH_4 flux in the peatland

The consistent reduction in CH_4 flux observed in the sedges *B. sinocompressus*, *C. muliensis* and *C. myosuroides* under darkened conditions (Figure 5a) demonstrates that light availability regulates CH_4 emissions across these species. However, clipping experiments revealed divergent mechanistic pathways underlying this common response. In *B. sinocompressus*, the stability of the flux after leaf removal, followed by a sharp decline upon stem sealing, indicates that the stem is the principal emission pathway. The darkening response in this species could therefore originate from physiological changes that increase resistance to gas diffusion along the stem transport, rather than stomatal closure at release sites. The lack of correlation between CH_4 flux and leaf area further supports that leaf-associated processes are not limiting emissions. As the highest-emitting species, its substantial CH_4 transport is likely facilitated by a well-developed, wheel-shaped schizogeny aerenchyma in the primary roots (Figure 6b). However, the dense exodermis in the primary roots (Figure 6e) appears to create a below-ground bottleneck that strongly restricts CH_4 entry from the rhizosphere. It is likely that thinner fine roots serve as the primary sites of CH_4 uptake, matching many earlier studies (Ge et al., 2024; Kutzbach et al., 2004).

The absence of a clipping effect in *C. myosuroides* similarly indicates that leaves do not restrain CH_4 release in this species either. The reduction in flux during darkening likely results from light-regulated modulation of internal gas transport efficiency, as it has even been suggested that wetland plants adapted to permanently high water levels have lost their ability to stomatal control (Ge et al., 2024). As with *B. sinocompressus*, the thick exodermis in *C. myosuroides*' primary roots may control CH_4 uptake (Figure 7e), suggesting that below-ground tissue properties could govern transport capacity.

In contrast, *C. muliensis* exhibited increased emissions after clipping (Figure 5b), suggesting that its leaves function as a restrictive barrier for CH_4 release. This observation is consistent with previous studies suggesting that leaf-level processes can regulate methane emissions in wetland (Morrissey et al., 1993; Schimel, 1995). This restriction aligns with the small aerenchyma and their limited connectivity in leaves (Figure 8d). Notably, the absence of a correlation between leaf area and emission rate (Figure 5c) further supports that CH_4 conductance in this species is determined by the internal leaf morphology, rather than by total leaf area. Darkening may further intensify this inherent leaf-based restriction. Despite possessing a high stomatal density, which reduces diffusive resistance at the surface, the internal structural bottleneck remains uncompensated. Additional factors, including rhizospheric CH_4 production and oxidation (Chen et al., 2009; Fritz et al., 2011), diameter of shoot base (Jackson, 1989), or shoot:root ratio (Jackson, 1994) may also contribute to the poor correlation between leaf area and CH_4 flux.

From a methodological perspective, our results highlight a critical limitation of traditional chamber-based measurements where CH_4 flux is determined from gas samples collected over extended intervals (e.g. 5, 15, 25 and 35 min) for analysis by gas chromatography (Ding et al., 2005; King et al., 1998; Yang et al., 2022). According to our results from the shading experiment, these at least half-hour measurements and the prolonged darkness, increasing CO_2 concentration, temperature and relative humidity could change plant physiology and bias the CH_4 flux (Nobel, 1999). Using a fast greenhouse gas analyser like in our study that can measure gas concentration changes in less than 10 min after closure may be a better option (Kohl et al., 2023; Tenhovirta et al., 2022; Zhang et al., 2020).

The poor correlation between CH_4 flux and leaf area (Figure 5c) also questions the common practice of using leaf area to normalize CH_4 flux across species (Ge et al., 2023; Ge, Korrensalo, et al., 2025; Villa et al., 2020). Also, current process-based models use leaf area index as an input when estimating plant-mediated CH_4 emissions (Raivonen et al., 2017; Wania et al., 2010). The wide use of leaf area (index) can be owing to two reasons: (i) leaf area is a simple, easy-to-measure parameter and also represents the size of specimens; and (ii) in most cases, the limiting interphase for the measured species is unknown. For this situation, option one is not to normalize at all, which may not be optimal since it ignores the variation in size or developmental stage of the plants. Option two is to use the parameters we can measure and have measured, for example, leaf area, the diameter of shoot base, shoot:root ratio, area of permeable root surface and root density, which could be better proxies for the limiting interphase.

5 | CONCLUSIONS

This study demonstrates that plants in alpine meadows predominantly function as CH_4 sinks, while those in peatlands act as CH_4 sources, with significant species-specific variation in transport mechanisms. Experimental warming reduced CH_4 uptake in meadow species but did not affect fluxes in peatland plants, indicating divergent ecosystem-level responses to climate change. Mechanistic experiments revealed that gas transport is constrained by below-ground root exodermis in *Blysmus sinocompressus* and *Carex myosuroides*, whereas leaf anatomy limits emissions in *Carex muliensis*. Critically, CH_4 flux showed no correlation with leaf area across species, challenging the use of leaf area index in CH_4 models. These findings highlight the necessity of incorporating species-specific functional traits and below-ground processes into predictive models of plant-mediated CH_4 emissions. Future efforts should focus on quantifying trait-based fluxes and understanding long-term vegetation and microbial feedbacks to improve climate projections.

AUTHOR CONTRIBUTIONS

Mengyu Ge, Raija Laiho and Aino Korrensalo conceived the ideas and designed the methodology; Mengyu Ge collected the data; Mengyu Ge analysed the data; Mengyu Ge led the writing of the manuscript; and Raija Laiho, Aino Korrensalo, Weifeng Wang, Jinsong Wang and Shuli Niu contributed critically to the drafts. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing financial interests or personal relationships that could have influenced this work. Shuli Niu is an Associate Editor of *Functional Ecology* but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.x95x69pz6 (Ge, Laiho, et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Summary of experimental design across three consecutive experiments in an alpine meadow and peatland on the Qinghai-Tibetan Plateau.

Table S2. Summary statistics for Tukey method to compare the estimates of plant CH_4 flux of the sedges (a) and forbs (b) under different warming treatments in the Zoige peatland. These estimates fitted from linear mixed effect models.

Table S3. Summary statistics for Tukey method to compare the estimates of plant CH_4 flux under different warming treatments in the alpine meadow. These estimates fitted from linear mixed effect models. *p* values denote statistical significance: **, 0.01; ***, 0.001.

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