

Research Article

Environmental Factors and Soil CO₂ Emissions in an Alpine Swamp Meadow Ecosystem on the Tibetan Plateau in Response to Experimental Warming

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We examined the response of soil CO₂ emissions to warming and environmental control mechanisms in an alpine swamp meadow ecosystem on the Tibetan Plateau. Experimental warming treatments were performed in an alpine swamp meadow ecosystem using two open-top chambers (OTCs) 40 cm (OA) and 80 cm (OB) tall. The results indicate that temperatures were increased by 2.79°C in OA and 4.96°C in OB, that ecosystem CO₂ efflux showed remarkable seasonal variations in the control (CK) and the two warming treatments, and that all three systems yielded peak values in August of 123.6, 142.3, and 166.2 g C m⁻² month⁻¹. Annual CO₂ efflux also showed a gradual upward trend with increased warming: OB (684.1 g C m⁻² year⁻¹) > OA (580.7 g C m⁻² year⁻¹) > CK (473.3 g C m⁻² year⁻¹). Path analysis revealed that the 5 cm depth soil temperature was the most important environmental factor affecting soil CO₂ emissions in the three systems.

1. Introduction

Sharp increase in the concentrations of atmospheric carbon dioxide (CO₂) and other greenhouse gases has led to a global average temperature increase of 0.76°C [1]. This scenario is more significant at high elevations and latitudes [2]. Areas with temperature increases of more than 1–2°C over the 30-year period of 1965–1995 were located primarily at latitudes greater than 50° north [1]. At high elevations and latitudes, climate warming will cause degradation of permafrost and affect plant phenology and precipitation patterns [3–5]. Warming can facilitate the decomposition of a large amount of organic carbon previously sequestered in the permafrost, thereby allowing gaseous carbon to enter the atmosphere and accelerating the process of global warming [6]. Therefore, accurate predictions of the impact of future climate change on the carbon cycle depend on accurate assessments of ecosystem

respiration in response to warming at high elevations and latitudes [7]. Ecologists have made the effect of warming on high altitude and high latitude ecosystems the topic of much current research [8–10]. Mertens et al. (2001) [11] monitored net ecosystem CO₂ exchange in tundra under warmed conditions in Greenland: a temperature increase of 2.5°C caused the tundra ecosystem to act as a carbon source and caused a 39% increase in belowground respiration. Mertens et al. [11] investigated trends in CO₂ exchange at the end of the growing season due to a temperature increase of 2.5°C at a tundra site: the elevated temperature significantly increased the rate of soil respiration, whereas gross photosynthesis by vegetation was less affected by the simulated warming. Welker et al. [12] used open-top chambers (OTCs) to raise the temperature 1–3°C above ambient temperatures and monitored the net exchange in a Canadian alpine ecosystem over a 9-year period. The elevated temperature increased the near-surface volume fraction

and significantly enhanced gross ecosystem photosynthesis, thereby causing the ecosystem to gradually change from a carbon source to a carbon sink. Biasi et al. [13] conducted a 2-year study of experimental warming using OTCs and found that warming promoted tundra ecosystem respiration, leading to a decrease in soil carbon and an increase in nitrogen content. Despite a marked decrease in the carbon/nitrogen ratio, there were no significant changes in the number and composition of soil microbes. The findings suggested that the tundra ecosystem will change from a carbon sink to a carbon source with future warming. Wu et al. [14] summarized 85 studies of experimental warming performed worldwide, which involved various terrestrial ecosystems such as forests, tundra, temperate grassland, mountain meadows, and shrubland. The relationship between net CO₂ exchange and warming in the various ecosystems was evaluated via a meta-analysis. It was concluded that warming promotes photosynthesis and respiration; however, it has no significant effect on net carbon absorption by the entire ecosystem.

Heating methods for ecosystem warming include field-style greenhouses, tents and open-top chambers (OTCs) of various shapes and sizes, soil heating pipes and cables, infrared reflector, and infrared radiator [15], in which the OTC is an experimental warming first used by the International Tundra Experiment to study the influence of global warming to high altitude and latitude region ecosystems [16]. The advantages of OTC warming equipment are low cost, convenient operation, easy repeatability, fitting to long-term field experiments, and minimal disturbance of the soil at the experiment site.

The Tibetan Plateau is located in southwestern China and spans an area of $\sim 250 \times 10^4$ km², that is, $\sim 25\%$ of the territory of China. The average elevation of the Tibetan Plateau exceeds 4000 m, making it the world's highest plateau [17]. In this region, swamp meadow spans an area of 4.9×10^4 km² and accounts for 1.96% of the plateau, making it one of the most extensive grassland ecosystems on the Tibetan Plateau [18]. These alpine ecosystems have developed in the extreme environments of the plateau and mountains. Due to their inherent vulnerability and instability, alpine ecosystems are extremely sensitive to human disturbance and global warming. Investigating the response of alpine ecosystems to rising temperatures is therefore highly valuable [18]. There have been studies of greenhouse gas fluxes in grassland ecosystems of the Tibetan Plateau. However, these studies have focused primarily on monitoring and investigating flux dynamics of greenhouse gases (particularly CO₂) in various types of alpine grassland ecosystems [19–21]. Little research has involved the effects of global climate change (particularly warming) on carbon fluxes in alpine swamp ecosystems. Studies elsewhere in the world have shown that key processes in the carbon cycle display significant responses to global warming in various ecosystems [22–24]. In the present study, we used an OTC system to perform experimental warming treatments to analyze soil CO₂ emissions dynamics and their relationships with environmental factors in an alpine swamp ecosystem on the Tibetan Plateau. This study has implications for understanding the carbon cycle in grassland ecosystems and in terrestrial ecosystems in general in China.

2. Material and Methods

2.1. Study Site. The study site was located in a swamp meadow of *Koeleria tibetica* in Dawu Town of Maqin County, Golog Tibetan Autonomous Prefecture, Qinghai Province, China. The swamp meadow is in the Sanjiangyuan region in the hinterlands of the Tibetan Plateau. The site coordinates are 34°27.569'N and 100°13.065'E. The meadow is at an elevation of 3700–4020 m, with a relief of 200–300 m, and measures 25 km north to south. The region has a continental plateau climate. The weather is cold and dry, and air pressures are low. The spring and autumn are short, and the freezing period lasts from October to the next April. The permafrost is generally 50–120 cm thick, and its upper limit is at a depth of 0.8–2.5 m. The growing season spans from May to September. The annual average temperature is -5.6 – 3.8 °C, with an extreme maximum of 28°C and an extreme minimum of -48 °C. The multiyear average precipitation is 155.35–697.93 mm and more than 75% of the rainfall falls from June to September. The annual average evaporation is 730–1700 mm, and the average relative humidity is 55%. The maximum wind speed is 31 m·s⁻¹, and the prevailing wind is westerly. The average number of days with thunderstorms is 47.8 per year [25].

In the study site, the plants are predominantly perennial mesophytic herbs. The dominant species of the grass community include *Kobresia littledalei*, *Carex moorcroftii*, *Festuca ovina*, *Kobresia pygmaea*, *Kobresia capillifolia*, *Kobresia bellardii*, and *Kobresia graminifolia*. The vegetation cover is greater than 90%. The predominant soil type is swampy soil with a maximum depth of 2.3 m. The soil pH ranges from 5.3 to 8.5. The soil contains 6.0–359 g kg⁻¹ organic matter, 0.2–14.9 g kg⁻¹ total nitrogen, 0.22–1.0 g kg⁻¹ total phosphorus, and 8.0–35.2 g kg⁻¹ total potassium [18].

2.2. Determination of Soil CO₂ Efflux and Micrometeorological Factors. The experiment was conducted from January 1 to December 31, 2012. Three plots with similar vegetation and aboveground biomass were selected at the study site. At two of the plots, two types of OTCs with a hexagonal cone structure were installed. The hexagonal surfaces were made of plexiglass with light transmittance of 95%. The OTCs were 40 cm (OA) and 80 cm (OB) tall. There was a 60 cm opening on the cone, and all sides of the cone were positioned at an angle of 60° from horizontal. The opening design ensured that the systems received the same amount of precipitation during rainfall. The third plot was left untreated and served as a natural control (CK). Each treatment was provided with three replicates. Air temperatures within the plots were monitored using an air hygrothermograph (HMP45AC, Vaisala, Finland) mounted 20 cm above the ground. Data were collected automatically every 30 min using data loggers (CR5000, Campbell Scientific Inc., Logan, UT, USA).

During the experiment, CO₂ efflux from the plots was measured using an open-type soil carbon flux measurement system (LI-8100, LI-COR Inc., USA). For the first measurement, the soil collar was embedded into the soil 1 day in advance to avoid short-term fluctuations in system respiration due to the OTC installation. The soil collar was a PVC cylinder 20 cm in base diameter and 10 cm tall, embedded

7 cm into the soil. The frequency of observation was as follows: during the vegetation growing season (May–September), diurnal variations were measured once every 7 days. During the nongrowing season (January–April and October–December), diurnal variations were measured once every 15 days. These measurements were taken from 8:00 to 8:00 the next day at 2-h intervals. The cumulative values measured on all days during a month were averaged and then multiplied by the number of days in the month to obtain the cumulative value for the month.

The soil temperature at a depth of 5 cm was measured using a soil thermocouple (105T, Campbell Scientific Inc.). The soil water content was measured using frequency-domain reflectometers (CS616, Campbell Scientific Inc.) with an accuracy of $\pm 2\%$. The reflectometers were buried at depths of 5, 20, 40, and 60 cm. The resulting soil water content is the volumetric water content of unfrozen water in the soil. These sensors were installed directly below the top openings of the OTCs in the geometric center of the plots to minimize the blocking of rainfall by the OTCs and thus reduce systematic errors in the results. All soil temperature, soil water content, and air temperature data were automatically collected every 30 min by the data loggers.

2.3. Determination of Biomass. From April to October 2012, the aboveground biomass, belowground biomass, and soil organic matter in each plot were measured on the 15th of each month. The aboveground biomass was measured using the harvest method. In OA and OB and at plot CK, we delineated 15 cm \times 15 cm quadrats. The vegetation in each quadrat was cut evenly from the roots, placed in bags, and numbered. Belowground live roots were collected from depth intervals of 0–10 cm, 10–20 cm, and 20–40 cm using a 5 cm diameter soil auger. The soil was washed through a 1-mm mesh sieve. All the aboveground and belowground samples were transported to the laboratory. The samples were dried at 65°C in an oven to constant weight and then weighed (g/m^2) three times for each treatment.

2.4. Statistical Analysis. The data were statistically analyzed using SAS 9.4 software (SAS Institute Inc., Cary, NC, USA). Significant differences between the treatments were tested using one-way ANOVA. The relationships between CO_2 efflux and environmental factors were evaluated using path analysis. Path analysis is the continuation of the simple correlation coefficient and decomposes the correlation coefficient on the basis of multiple regression. It uses direct and indirect paths to indicate the direct effect of a variable on a dependent variable and the indirect effects of other variables on a dependent variable [26, 27]. In path analysis, the decision coefficient $R_{(j)}^2$ is often used to quantify the integrated determination effect of environmental factors (x_j) on soil CO_2 emissions (y). $R_{(j)}^2$ contains not only the direct determination effect R_j^2 of x_j on y but also the indirect determination coefficient related to x_j :

$$R_{(j)}^2 = R_j^2 + \sum_{j \neq i} R_{ji}^2 \quad (1)$$

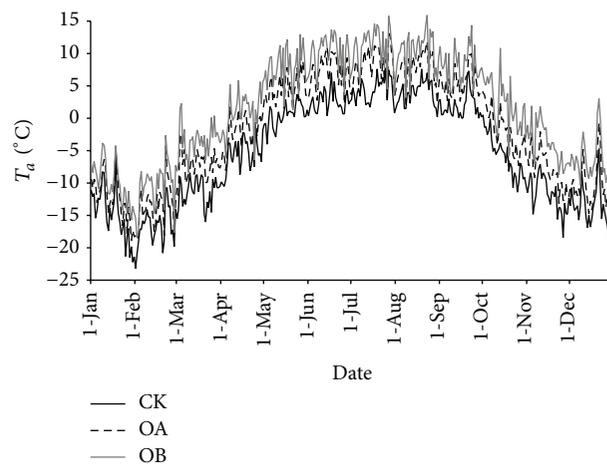


FIGURE 1: Seasonal variations in the air temperature of the alpine swamp ecosystem corresponding to the warming treatments.

3. Results and Discussion

3.1. Changes in Environmental Factors. Inside the OTCs, wind velocities, air turbulence, and heat dissipation were reduced. These reductions and the penetration of solar infrared radiation through the glass walls caused warming in the OTCs [28]. Temperature measurements in the three systems indicated that the daily average air temperatures (T_a) in OA and OB increased significantly ($F = 46.52$, $P < 0.001$) compared with those at the control plot (CK). The T_a values were 2.79°C and 4.96°C higher in OA and OB than that at plot CK, respectively (Figure 1). According to Yu [29], the annual average air temperature on the Tibetan Plateau rose 0.7°C every 10 years from 1981 to 2010. The warming systems used in the current study are therefore representative of the significant warming expected over the next 40–70 years.

Due to the high air temperature and weak air circulation within the OTCs, the 5 cm soil temperature (T_{soil}) was elevated. As shown in Figure 2, T_{soil} was 1.01°C and 3.04°C higher in OA and OB than that at plot CK, respectively, and these differences were statistically significant ($F = 16.938$, $P < 0.001$).

Meanwhile, the elevated air temperature and soil temperature accelerated the evaporation of soil water and the transpiration of plants, resulting in a lower water content in the surface soil in the OTCs. As shown in Figure 3, the daily average 5 cm soil water content (SWC) was less in OB than in OA (2.2%) and CK (4.9%); these differences were statistically significant ($F = 58.936$, $P < 0.001$).

3.2. Changes in Biological Factors. In this study, the experimental treatments with different magnitudes of warming had significant effects on biomass production in the alpine swamp meadow ecosystem (Figures 4 and 5). Continued warming resulted in significant increases in the aboveground and belowground biomass in OA and OB relative to plot CK. During the growing season, the aboveground biomass increased by 21.1–76.4% and 44.9–168.2% in OA and OB, respectively, and the belowground biomass increased by 47.3–60.2% and

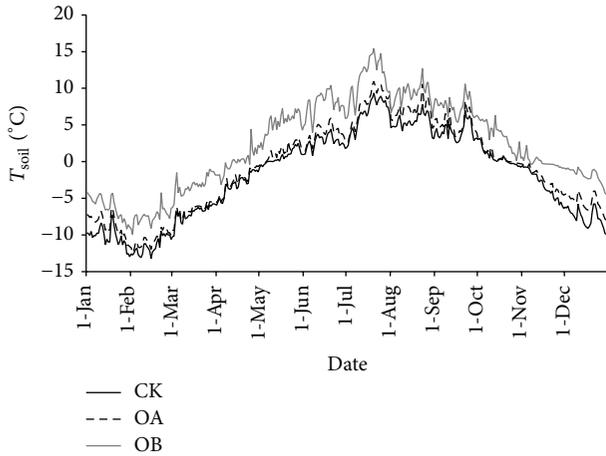


FIGURE 2: Seasonal variations in 5 cm depth soil temperature corresponding to the warming treatments.

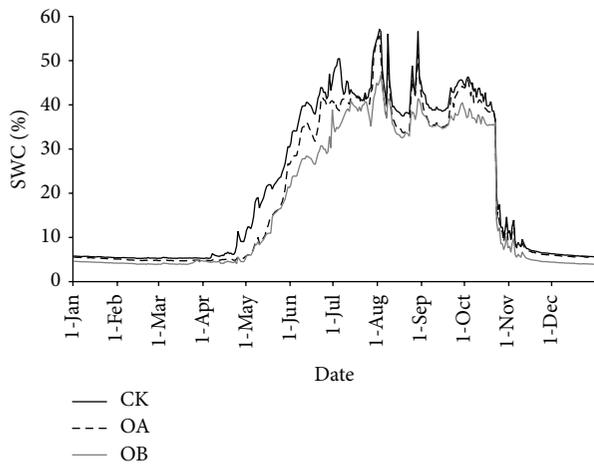


FIGURE 3: Seasonal variations in 5 cm depth soil water content corresponding to the warming treatments.

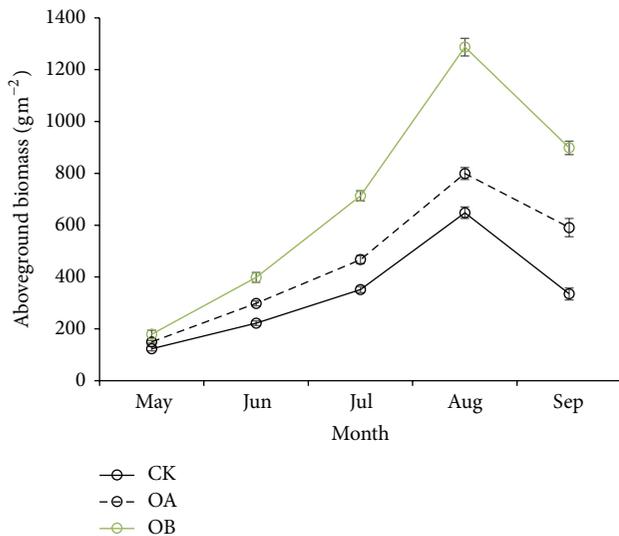


FIGURE 4: Growing season variations in aboveground plant biomass corresponding to the warming treatments.

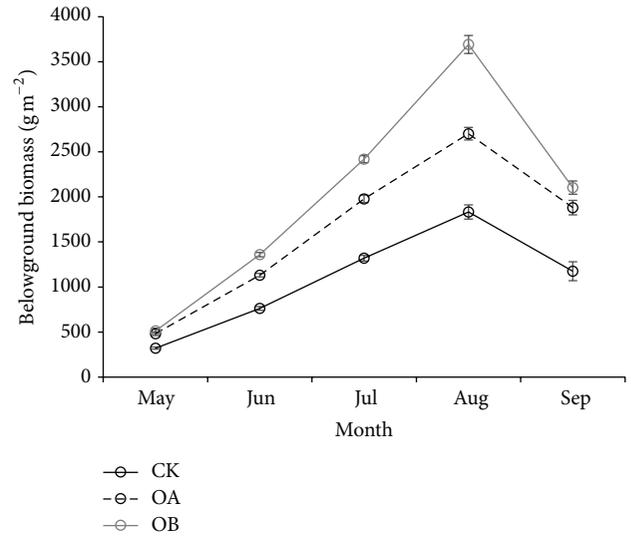


FIGURE 5: Growing season variations in belowground plant biomass corresponding to the warming treatments.

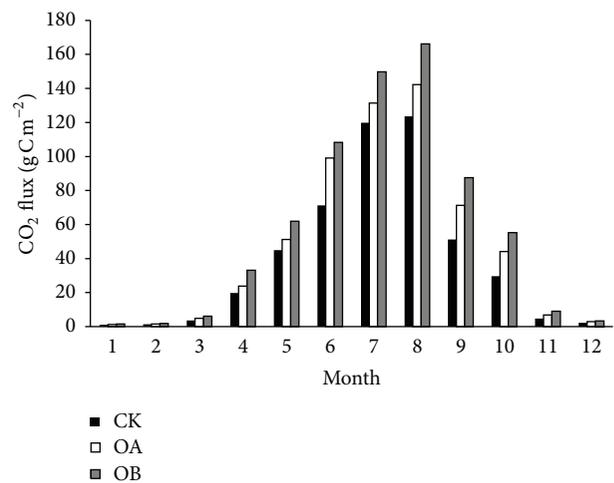


FIGURE 6: Seasonal variations in CO_2 efflux corresponding to the warming treatments.

59.0–101.3% in these two OTCs, respectively, compared to that in plot CK. Thus, the short-term warming had a positive effect on the vegetation biomass in this alpine swamp meadow. This trend is attributed to changes in the microclimate of the plant community produced by the OTCs. To a certain extent, these changes satisfied the demand for heat for plant growth and benefitted the growth and development of the plants [30]. The current result is consistent with previous findings by Jonasson et al. [31], who reported a significant correlation between warming and plant growth, at least in the short term.

3.3. Effect of Warming on CO_2 Efflux. The carbon emissions in the alpine swamp meadow ecosystem exhibited significant seasonal variations (Figure 6). The carbon emissions during the distinct stages of plant development in all three systems

(CK, OA, and OB) ranked as follows: vigorously growing stage (July-August) > rapidly growing stage (June) > yellowing stage (September) > reviving stage (April-May). The highest ecosystem carbon emissions in the three systems occurred in August: 123.6, 142.3, and 166.2 g C m⁻² month⁻¹ in CK, OA, and OB, respectively. During the nongrowing season, ecosystem carbon emissions remained relatively low in all three systems. Because respiration by grassland ecosystems is closely associated with air temperatures, respiration by their plant roots and soil microbes is sensitive to soil temperature variations [32]. In the current study site, rainfall and air temperatures were at maximums during the vigorously growing stage (July-August). These synchronous hydration and thermal conditions contributed to the high levels of plant respiration and soil microbial activity.

The warming also had a significant effect on CO₂ efflux from the swamp meadow ecosystem (Figure 6). CO₂ efflux was ranked as follows: OB (684.1 g C m⁻² year⁻¹) > OA (580.7 g C m⁻² year⁻¹) > CK (473.3 g C m⁻² year⁻¹). Greater warming led to greater ecosystem respiration. This result is consistent with the conclusion developed by Hobbie and Chaimn III [33], who performed an experimental warming study under greenhouse conditions in a permafrost tundra site in Alaska. Hobbie and Chaimn III [33] suggested that warming enhances plant respiration and increases the population and activity of microbes; these mechanisms accelerate the decomposition of soil carbonaceous materials and thereby increase CO₂ efflux.

3.4. Effects of Environmental Factors on CO₂ Efflux. Path analysis is the analysis of relationships between the independent variables and between independent and dependent variables. It indicates direct and indirect effects of independent variables on a dependent variable [26, 27]. Path analysis solves the one-sidedness of multiple correlation analysis by including the effects of additional variables in a linear correlation of any two variables. It also addresses the defect of multiple regression analysis that cannot directly compare the effect of a cause on a result due to the inclusion of a unit for partial regression coefficients. Path analysis thus allows one to quantify the contributions of several environmental factors to ecosystem CO₂ [34].

In the present study, path analysis was conducted to evaluate the relationship between various environmental factors and soil CO₂ emissions in the CK, OA, and OB systems during the growing season. In the three systems, T_{soil} was the most important environmental factor controlling soil CO₂ emissions in the alpine swamp meadow ecosystem. The direct path coefficients of T_{soil} for soil CO₂ emissions were 0.53, 0.59, and 0.63, and the total path coefficients were 0.52, 0.72, and 0.89 (Figure 7). These values all represented contributions greater than those of other environmental factors to soil CO₂ emissions in this ecosystem. This conclusion agrees with the conclusions of Zhao et al. [20] and Bai et al. [25]. Temperature is an important factor regulating several ecological processes and properties associated with ecosystem respiration. These processes and properties include root development, evapotranspiration, and soil water content [35, 36]. Mielnick and

Dugas [37] concluded that if only temperature factors are taken into consideration, 46% of the variation in soil respiration is due to variations in soil temperature.

The effect of SWC on ecosystem respiration is complex. Very different findings have been obtained in different ecosystems. In the current study, the total path coefficients of SWC for soil CO₂ emissions were -0.35 (CK), -0.22 (OA), and -0.14 (OB) (Figure 7). These values indicate that the SWC is a major factor limiting soil CO₂ emissions in these three systems, consistent with findings by Kato et al. [19] from an alpine meadow ecosystem in Haibei station. Kato et al. [19] concluded that a 30% SWC produces maximum carbon emissions in alpine meadow ecosystems on the Tibetan Plateau. A SWC exceeding this value can hinder O₂ diffusion in the soil, thereby inhibiting organic matter decomposition and microbial respiration [38]. In the current study, the experimental plots were located in a humid natural environment, and the SWC was constantly at supersaturation throughout the growing season and thus unfavorable for soil microbial respiration. Thus, the SWC is an important environmental factor inhibiting soil CO₂ emissions in this ecosystem. We also noted that the total path coefficients of SWC for CO₂ successively increased in the CK, OA, and OB systems. These results indicate that the inhibition of soil CO₂ emissions by soil water decreases with warming. This relationship exists because warming promotes evapotranspiration and reduces the SWC. With future climate warming, an SWC decrease will also be an important contributor to soil CO₂ emissions in alpine swamp ecosystems.

In the CK, OA, and OB systems, T_a was not the most important environmental factor affecting ecosystem CO₂ emissions. However, the changes in other factors due to the T_a increase had a more profound impact on ecosystem respiration. This study spanned only one year, and more-extensive work has not yet been performed regarding the effects of warming on carbon emissions in alpine swamp meadow ecosystems. Additional studies of this type should be conducted.

4. Conclusions

Warming had a significant effect on carbon emissions from the swamp meadow ecosystem of the Sanjiangyuan region. Annual soil CO₂ emissions in OA and OB were, respectively, 22.7% and 44.5% greater than those in plot CK. The warming effect was more evident in OB, resulting in higher air and soil temperatures and a lower soil water content, which were conducive to the decomposition of soil organic matter and the production of CO₂. Ecosystem carbon emissions were jointly affected by multiple environmental factors. Path analysis indicated that temperature and soil water were the two most important factors affecting soil CO₂ emissions at the study site. With global climate change, temperature and precipitation patterns will change in this region. Such changes will in turn act on the local carbon cycle and have additional deleterious effects on the local climate. Therefore, the Chinese government should devote attention to and support the monitoring of carbon cycle processes in various ecosystems on the Tibetan Plateau.

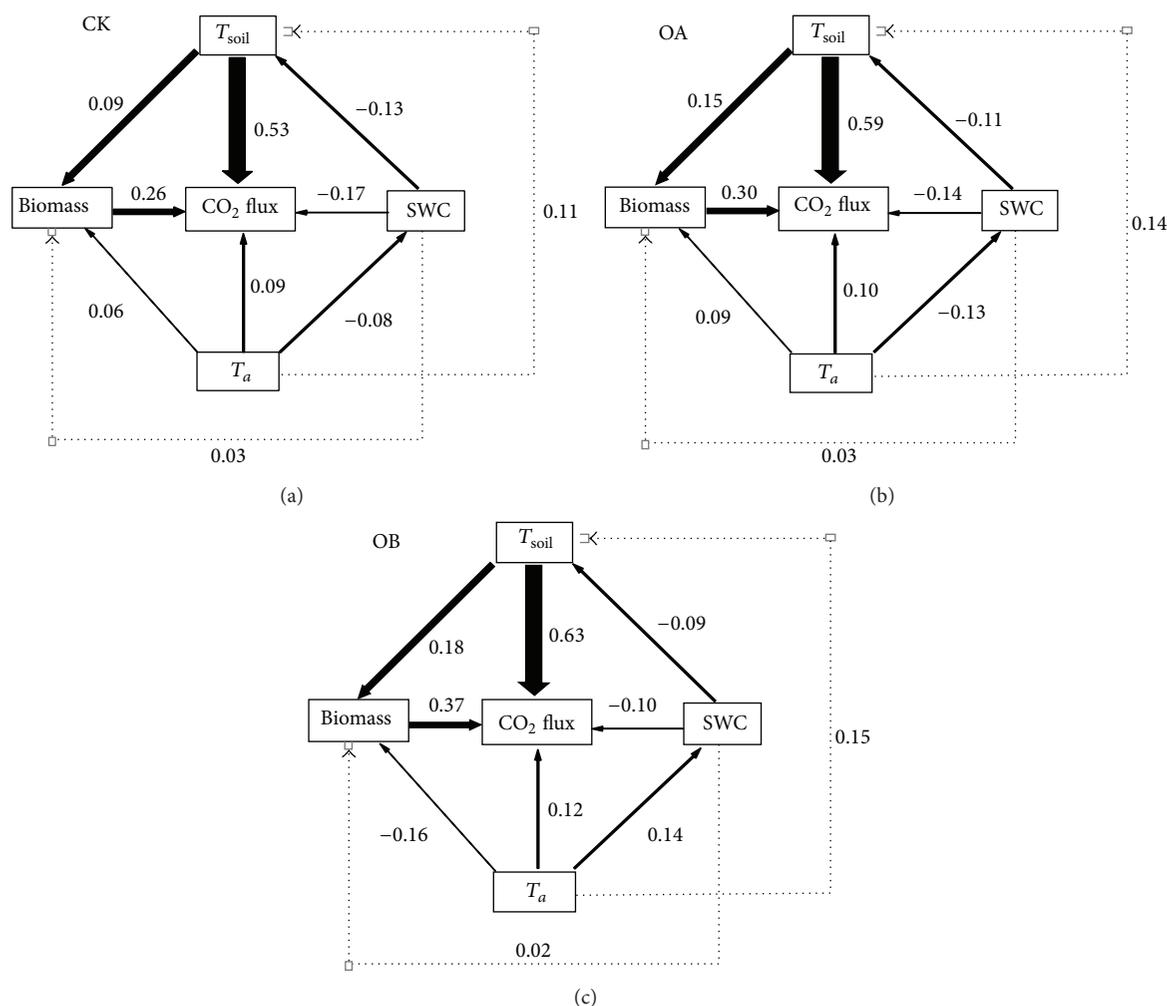


FIGURE 7: Path diagrams showing the effects of air temperature (T_a), 5 cm depth soil temperature (T_{soil}), 5 cm depth soil water content (SWC), and plant biomass (biomass) on ecosystem CO_2 efflux (CO_2 flux) during the growing season in plot CK (a), OA (b), and OB (c). The thicknesses of the arrows and the adjacent values represent the path coefficients. The analysis was based on the daily average values of all variables.

Competing Interests

The authors declare that they have no competing interests.

Acknowledgments

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