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Temperature Matters More than Fertilization for Straw Decomposition in the Soil of Greenhouse Vegetable Field

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Abstract: As the largest organic carbon input to agroecosystems, crop straw can solve the problem of soil quality degradation in greenhouse vegetable fields, harmonize the balance between soil nutrients and energy, and improve soil quality to maintain the sustainable production of greenhouse vegetables. However, the microbial mechanism of the straw decomposition process under different temperatures and fertilization treatments in greenhouse vegetable soils has not been clarified. Soil samples were used to investigate the biology of straw decomposition in the soil at three incubation temperatures (15, 25, and 35 °C) through a soil incubation experiment (60 d) under different fertilization treatments. Fertilization treatments for this long-term field experiment included chemical fertilizer (CF), substitution of half of the chemical N fertilizer with manure (CM), straw (CS), or combined manure and straw (CMS). The results showed that soil hydrolase activities tended to decrease with increasing temperature during straw decomposition. Compared with the CF, organic substitutions (CM, CMS, and CS) increased soil β-glucosidase, β-cellobiosidase, N-acetyl-glucosaminidase, and β-xylosidase activities during straw decomposition. Soil CO_2 emission rates were the highest at each incubation temperature on the first day, rapidly declining at 25 °C and 35 °C and slowly declining at 15 °C. The soil CO_2 cumulative emissions tended to increase with increasing temperature under different fertilization treatments. PCA showed that the responses of soil enzyme activities to temperature at 7, 15, and 30 d of straw decomposition were stronger than those of fertilization. In summary, both fertilization treatment and incubation temperature could influence soil CO_2 emissions by affecting soil physicochemical properties and enzyme activities during straw decomposition, whereas incubation temperature had a stronger effect on straw decomposition than fertilization, as indicated by PLS-PM and three-way ANOVA. Considering the influence for fertilization on the straw decomposition process at different incubation temperatures, the straw applications (CMS and CS) were more suitable to temperature changes.

Keywords: greenhouse vegetables; straw decomposition; incubation temperatures; fertilization treatments; enzyme activity

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1. Introduction

Currently, the study of soil carbon cycling in agroecosystems has become a popular concern for ecologists worldwide. Studies on the biochemical cycling of soil carbon have found that soil microorganisms affect the decomposition of fresh organic matter (e.g., plant residues) and thus the mineralization of organic carbon (CO_2 emissions) [1]. Crop residues are rich in mineral nutrients and organic matter, which can enrich soil microbial community diversity, improve soil fertility, and increase crop yield [2–4]. Crop straw (high C/N) can harmonize the balance between soil nutrients and energy (carbon) and improve soil quality to maintain the efficient and sustainable production of greenhouse vegetables [5]. However,

there are few studies available on the microbial mechanism of straw decomposition in greenhouse vegetable production.

After straw is returned to the soil, the organic components begin to decompose through microbial action. The process can be divided into four stages: carbohydrate decomposition, semi-cellulose decomposition, cellulose decomposition, and lignin decomposition. The decomposition process is accompanied by changes in soil enzyme activity and organic carbon mineralization [1,6,7]. Soil temperature, an important environmental factor, has a vital effect on straw decomposition [8–10]. Variations in soil temperature may have direct or indirect effects on soil carbon fluxes (soil heterotrophic and autotrophic microbial respiration), which in turn affect soil carbon fixation in agroecosystems [11,12].

Soil enzyme activity, an important index for evaluating soil quality, is involved in nutrient cycling and organic matter decomposition [13]. Soil enzyme activities at different temperatures have been well documented, and elevated soil temperatures affect soil enzyme activities associated with carbon and nitrogen transformations [13–15]. Meanwhile, elevated temperatures increase cellulolytic enzyme activities in the early stages of decomposition, whereas in the middle stages, they increase ligninolytic enzyme activities [16]. The trend of increasing soil N-acetyl-glucosaminidase and phosphatase activities and decreasing soil β-glucosidase was observed with increasing temperature [17]. However, there are few reports on the soil enzyme activities involved in straw decomposition at different temperatures. Previous studies have reported that the temperature sensitivity (Q_{10}) of soil enzyme activity is less than that of CO_2 emissions and that long-term warming reduces the temperature sensitivity of soil enzymes by decreasing the maximum potential activity (V_{max}) and increasing their half-saturation constant (K_m) [18–21]. Based on the unique high-temperature and high-humidity internal environment of greenhouse vegetables, there is an urgent need to study the changes in soil enzyme activity during straw decomposition at different temperatures.

Fertilization, an important measure in farm management, could alter soil physicochemical properties, which in turn improves the nutrients required for plant growth and increases crop yield [22–24]. Additionally, fertilization can affect the rate of straw decomposition by influencing the degradation of flora involved in the process of straw decomposition and by regulating soil nutrient effectiveness. Organic amendments (e.g., straw application) can increase soil microbial biomass and enzyme activity and then affect the straw decomposition rate [25,26]. Straw decomposition is a microbially mediated process, and long-term organic fertilization causes the soil to develop a specific microflora composition that enhances resistance to external environmental changes [27,28].

In this study, the effects of fertilization and temperature on soil enzyme activities and CO_2 emissions during straw decomposition were investigated using incubation experiments. We attempted to integrate these indicators to comprehensively illuminate the effects of incubation temperature and fertilization treatments on the straw decomposition process. Specifically, we hypothesized that there may be a certain fertilization treatment that can buffer the effect of temperature on straw decomposition in the long-term organic substitution fertilization of greenhouse vegetable production.

2. Materials and Methods

2.1. Experimental Site Description and Soil Sampling

The field experiment was implemented in 2009 at the Dahe experimental station (38°08′ N, 114°23′ E) in Hebei Province, China, where a winter–spring cucumber (*Cucumis sativus* L., c.v. Bomei No. 11) and autumn–winter tomato (*Lycopersicum esculentum* Mill., c.v. Jinpeng No. 11) rotation system was applied in greenhouse vegetable ecosystems. This region has a typical semi-humid continental monsoon climate, with a mean annual temperature of 11.5 °C and rainfall of 540 mm. The soils are classified as calcareous cinnamon soil with clay loam texture by FAO soil classification [29]. The basic soil properties (0–20 cm depth) are as follows: pH, 8.0; organic C, 5.3 g kg^{-1}; nitrate N, 18.3 mg kg^{-1}; available P, 6.2 mg kg^{-1}; and available K, 98.2 mg kg^{-1} [30].

Under the premise of equal amounts of nutrient (N, P_2O_5, and K_2O) inputs, fertilization treatments were applied in which manure-N (MN) and/or straw-N (SN) were used as substitutes for chemical-N (CN) to varying degrees: (1) 100% chemical N (CN) addition (CF), (2) 50% CN and 50% manure N (MN) addition (CM), (3) 50% CN, 25% MN, and 25% straw N (SN) addition (CMS), and (4) 50% CN and 50% SN addition (CS). The total amounts of N, P_2O_5, and K_2O applied to winter–spring cucumber were 600, 300, and 525 kg hm^{-2}, respectively, while the total amounts of N, P_2O_5, and K_2O applied to autumn–winter tomato were 450, 225, and 600 kg hm^{-2}, respectively. The specific N and carbon inputs in each treatment for winter–spring cucumber and autumn–winter tomato are shown in Table 1. Additional information on field location experiments is shown in Rong et al. [30].

Table 1. Nitrogen and carbon inputs in each fertilization treatment during the winter–spring cucumber season and autumn–winter tomato season (kg hm^{-2}).

Treatments	N Input				C Input		
	Chemical Fertilizer	Organic Manure	Corn Straw	Total	Organic Manure	Corn Straw	Total
			Winter–spring cucumber season				
CF	600.0	0	0	600.0	0	0	0
CM	300.0	300.0	0	600.0	2566.4	0	2566.4
CMS	300.0	150.0	150.0	600.0	1283.2	6482.8	7766.0
CS	300.0	0	300.0	600.0	0	12,965.5	12,965.5
			Autumn–winter tomato season				
CF	450.0	0	0	450.0	0	0	0
CM	225.0	225.0	0	450.0	1924.8	0	1924.8
CMS	225.0	112.5	112.5	450.0	962.4	4862.1	5824.5
CS	225.0	0	225.0	450.0	0	9724.2	9724.2

Soil samples (0–20 cm) were collected after uprooting the winter–spring cucumber plants in June 2021, which was the 24th cultivation season at the experimental site. Ten soil cores (diameter, 3 cm) were arranged in an "S" pattern and merged into a composite sample in each plot. Soil samples were sieved through a 2 mm mesh after the removal of stones and plant residues. One part was used for indoor incubation experiments. The other part was air-dried and passed through 1 mm mesh and 0.15 mm mesh, and the samples were used to determine the basic physicochemical parameters.

2.2. Laboratory Incubation

The incubation experiments were designed with two factors, namely the fertilization treatment factor (CF, CM, CMS, and CS) and the incubation temperature factor (15, 25, and 35 °C). Soil samples (equivalent to 20 g dry soil) and 0.1 g straw were transferred to 100 mL unsealed glass bottles. Simultaneously, an unamended soil sample (CK) without straw (c soil) was also prepared. The treatments were set up in 36 replicates (3 plot samples × 4 incubation periods × 3 incubation temperatures). Dark aerobic incubation experiments were carried out in artificial climate chambers at 15, 25, and 35 °C. Gas exchange inside and outside the bottle was allowed by maintaining 75% of the maximum field capacity, and the bottles were weighed once a week during the incubation process and replenished with water when the soil water loss exceeded 5% of the initial incubation soil weight. To reduce the influence of external conditions, the bottles were switched considering their position. Soil samples were collected destructively at 7, 15, 30, and 60 d, and gas samples were collected at 1, 3, 7, 15, 30, and 60 d during the incubation period.

2.3. Soil Extracellular Enzyme Activity (EEA) Analysis

Six soil EEAs, including β-glucosidase (βG), β-cellobiosidase (CBH), N-acetyl-glucosaminidase (NAG), β-xylosidase (XYL), α-glucosidase (αG), and leucine-aminopeptidase

(LAM), were measured through a microplate enzyme assay [31]. Two labeled fluorogenic substrates (4-methylumbelliferone-β-D-glucoside and 7-amino-4-methylocumarin) were used to determine enzyme activities. Briefly, soil samples (1.0 g in dry weight) were dissolved in 50 mL Na-acetate (50 mM) buffer to create a soil suspension. For soil EAA analysis, the buffer, soil suspension, 10 mM references, and 200 µM substrates were placed into the wells of a black 96-well microplate. The black 96-well microplates were incubated at 25 °C for 4 h in the dark. Afterward, 10 µL NaOH (1 M) solution was added immediately to each well to terminate the enzymatic reaction. Fluorescence was quantified by a microplate fluorometer (Scientific Fluoroskan Ascent FL, Thermo, Waltham, MA, USA) with 365 nm excitation and 450 nm emission filters (Table 2).

Table 2. Extracellular enzymes and their corresponding substrates.

Extracellular Enzyme	Substrate
α-Glucosidase	4-MUB-α-D-glucoside
β-Glucosidase	4-MUB-β-D-glucoside
β-Cellobiosidase	4-MUB-β-D-cellobioside
β-Xylosidase	4-MUB-β-D-xyloside
N-Acetyl- glucosaminidase	4-MUB-N-acetyl-β-D-glucosaminide
Leucine-aminopeptidase	L-Leucine-7-amino-4-methylcoumarin

2.4. Soil Carbon Dioxide (CO_2) Measurement and Calculation

Soil CO_2 was determined by collecting the gas at 0 h and 4 h after the wide-mouth bottle was closed, extracting the gas sample (22 mL) from the glass bottle with a syringe, and then transferring it to a vacuum serum bottle (10 mL). The CO_2 content was measured using an Agilent-8890a gas chromatograph (H8890a, Agilent Technologies, Sata Clara, CA, USA).

Soil CO_2 emissions were calculated using the following equation [32]:

$$F_{(\text{mg kg}^{-1}\cdot\text{d}^{-1})} = \frac{(C_4 - C_0) \times \text{V} \times 44 \times 273.15 \times 24}{22.4 \times (273.15 + T) \times (\text{W} \times 4 \times 1000)}$$

where C_0 and C_4 are the CO_2 concentrations (µL L^{-1}) in the bottle at 0 and 4 h, respectively, V is the volume of the wide-mouth bottle (0.1 L), 44 is the density of CO_2 in the standard state (kg m^{-3}), 273.15 is the gas equation constant, T is the temperature in the incubator, 22.4 is the molar volume of CO_2 in the standard state, and W is the soil quality in the glass bottle (0.02 kg).

The value of Q_{10} was calculated using the following equation [33]:

$$Q_{10} = \left(\frac{F_{T_1}}{F_{T_2}}\right)^{\left(\frac{10}{T_2 - T_1}\right)}$$

where F_{T_1} and F_{T_2} are the reaction rates of a reaction at temperatures T_1 and T_2, respectively, and T_1 and T_2 are the thermodynamic temperatures at which the reaction occurs.

2.5. Soil Physicochemical Analysis

Soil nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) were measured using a flow injection autoanalyzer (Smartchem 200, Alliance, Paris, France) after extraction by 2 M KCl [34]. Soil organic carbon (SOC) and total nitrogen (TN) were measured using an elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany). Soil pH was tested with a compound electrode (PE 10, Sartorius, Goettingen, Germany) in a soil/water ratio of 1:2.5. Soil dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were determined using a C/N analyzer (Multi N/C 3100/HT1300, Analytik Jena AG, Jena, Germany) by leaching with deionized water at 25 °C (soil/water ratio of 1:5) [35]. Soil available phosphorus (P) was extracted by 0.5 M $NaHCO_3$ (pH 8.5) and determined using the Olsen method [36]. Soil available potassium (K) was extracted by 1 MCH_3COONH_4

and tested using atomic absorption spectrometry (NovAA300, Analytik Jena AG, Jena, Germany) [37].

2.6. Statistical Analysis

One-way analysis of variance (ANOVA) with Duncan's multiple range test was applied to evaluate the significance ($p < 0.05$) of soil EEAs and CO_2 fluxes under different incubation temperatures and fertilization treatments using the SPSS 18.0 software (SPSS Inc., Chicago, IL, USA). Three-way analysis of the effects of incubation temperatures, fertilization treatments, and incubation periods on soil EEAs and CO_2 emissions during straw decomposition was performed using SPSS 18.0 software (SPSS Inc. Chicago, IL, USA). Principal component analysis (PCA) was performed on the composition of soil enzyme activity using CANOCO 5.0 software (Microcomputer Power, Inc., Ithaca, NY, USA). Partial least squares path modeling (PLS-PM) determined the relationships among the fertilization treatments, incubation temperatures, soil EEAs, physicochemical properties, and CO_2 emissions using R (v.3.6.1) with the "plspm" package.

3. Results

3.1. Soil Enzyme Activities during Straw Decomposition

As shown in Figure 1, soil CBH, XYL, and αG activities during straw decomposition (7, 15, 30, and 60 d) showed a decreasing trend with increasing temperature. Soil βG activity showed a decreasing trend with increasing temperature at 7, 15, and 30 d of straw decomposition, and soil βG activity at 35 °C was higher than that at 15 °C and 25 °C at 60 d of straw decomposition. Soil NAG and LAM activities at 15 °C and 25 °C were higher than those at 35 °C at 7 d of straw decomposition and decreased with increasing temperature at 15, 30, and 60 d of straw decomposition.

During straw decomposition (7, 15, 30, and 60 d), soil βG, CBH, NAG, and XYL activities in the organic substitutions (CM, CMS, and CS) were higher than those in the CF, among which soil βG, CBH, and XYL activities in the straw applications (CMS and CS) were higher than those in the manure applications. Compared to the CF treatment, the organic substitution treatments increased soil LAM activity at 7 d of straw decomposition and decreased soil LAM activity at 15 and 30 d. Meanwhile, soil LAM activity was the highest in the CMS at 60 d of straw decomposition. The αG activity of the CMS and CS was higher than that in the CF treatment at 7 and 15 d of straw decomposition, respectively. Organic substitutions increased soil αG activity at 30 and 60 d of straw decomposition, in which straw application (CMS and CS) was higher than manure application.

The soil βG, CBH, NAG, and XYL activities showed an overall decreasing trend as straw decomposition advanced. Meanwhile, the soil αG and LAM activities showed an overall increase initially and then decreased.

3.2. Principal Component Analysis of Soil Enzyme Activity during Straw Decomposition

Principal component analysis (PCA) revealed that temperature and fertilization treatment altered the composition of soil EEAs (Figure 2). Soil EEAs could be divided into two groups, i.e., one group at 15 °C and another group at 25 and 35 °C on days 7, 15, and 30, which indicated that soil enzyme activities respond more strongly to incubation temperature than to fertilization treatments. Furthermore, it was the fertilization treatments, rather than temperature, that divided soil enzyme activities into two groups at 60 days of straw decomposition, i.e., one group in the CF and CM treatments and another group in the CMS and CS treatments.

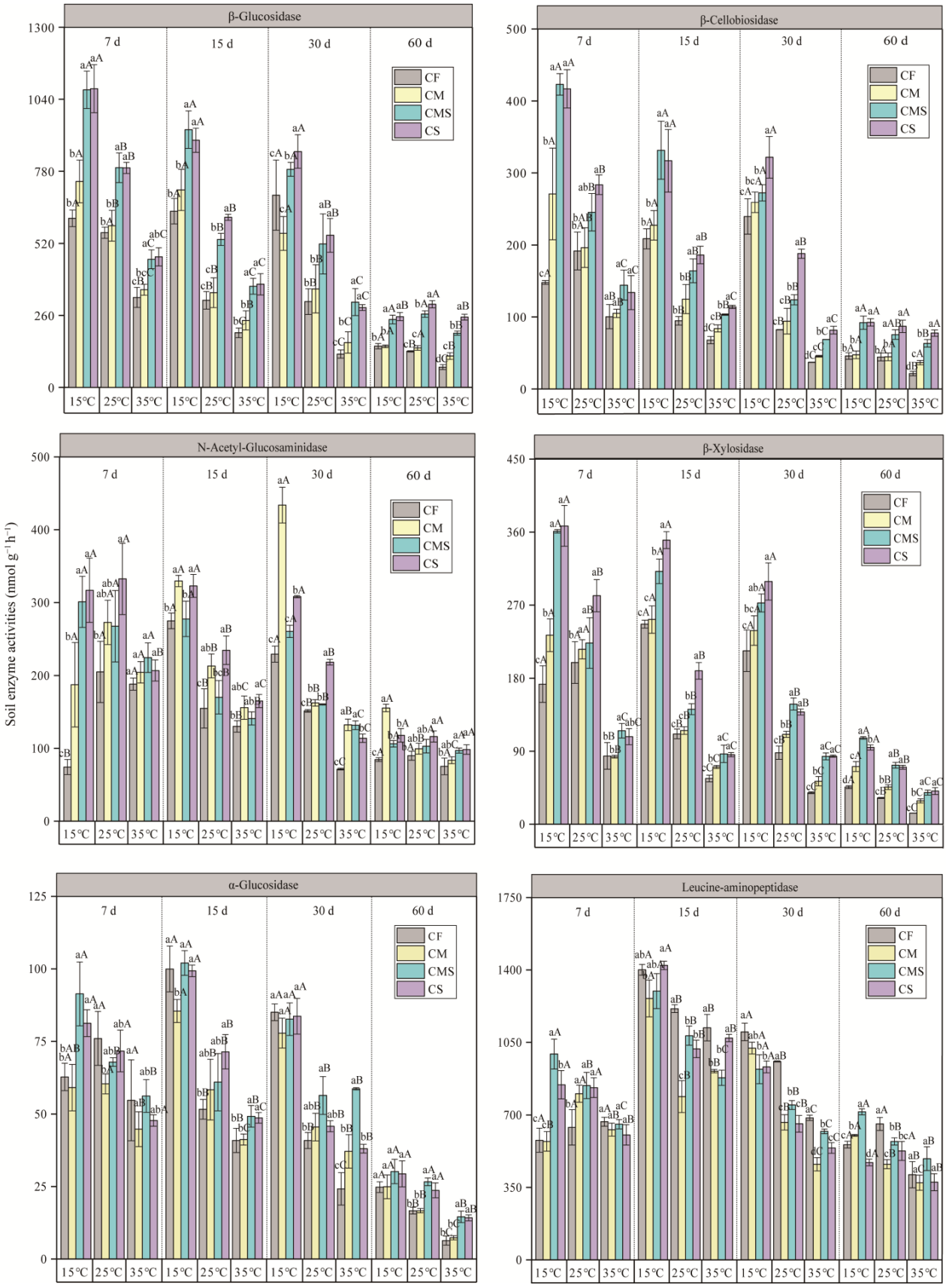

Figure 1. Changes in soil EEAs during straw decomposition under different fertilization treatments and incubation temperatures. Different lowercase letters indicate significant differences among the

different fertilization treatments under the same temperature condition (Duncan test, $p < 0.05$). Different uppercase letters indicate significant differences among the different temperatures under the same fertilization treatment (Duncan test, $p < 0.05$).

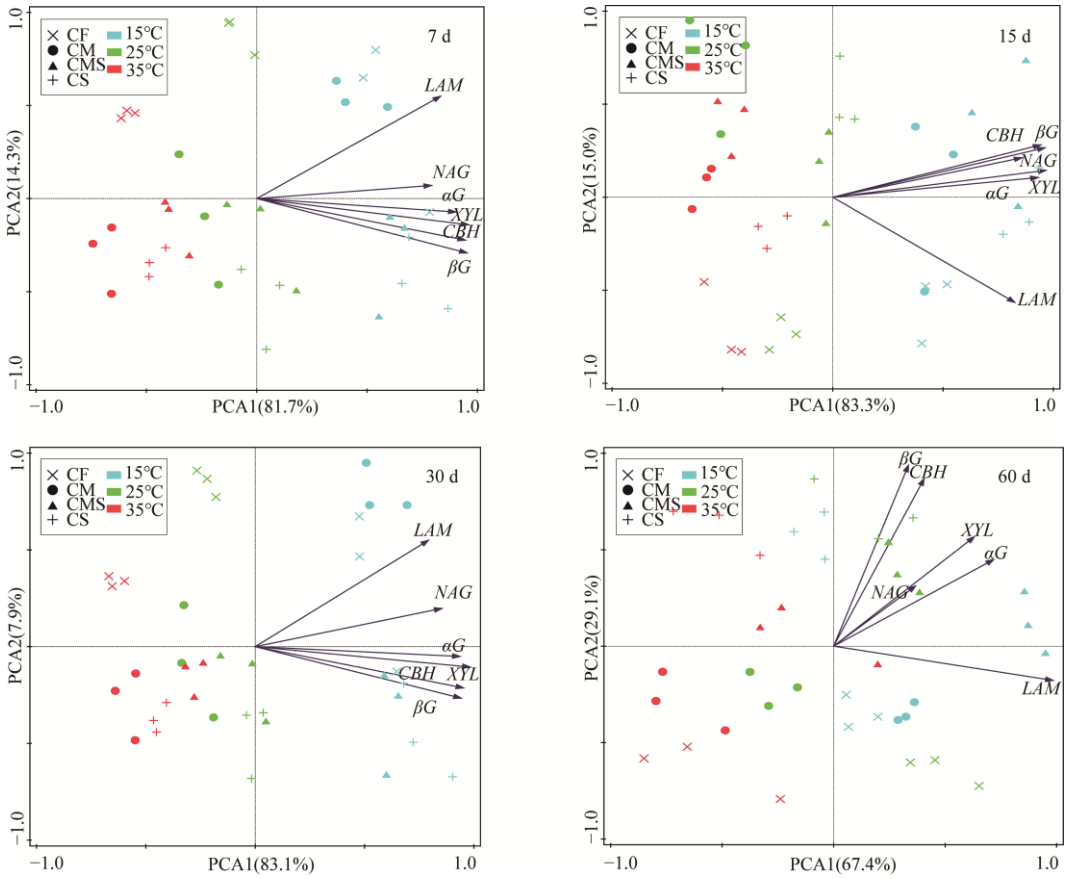

Figure 2. Principal component analysis (PCA) of soil EEAs during straw decomposition under different fertilization treatments and incubation temperatures. Abbreviations: βG, β-glucosidase; CBH, β-cellobiosidase; NAG, N-acetyl-glucosaminidase; XYL, β-xylosidase; αG, α-glucosidase; LAM, leucine-aminopeptidase.

3.3. Soil CO_2 Emission Fluxes during Straw Decomposition

The soil CO_2 emission rate at each incubation temperature was the highest on the 1st day of straw decomposition (Figure 3). Soil CO_2 emission rates rapidly declined until 7 d at 25 °C and 35 °C, slowly declined until 30 d at 15 °C, and remained stable thereafter. Soil CO_2 emission rates were higher at 25 °C and 35 °C than at 15 °C in 1, 3, and 30 d of straw decomposition, and the opposite tendency was found in 7 and 15 d of straw decomposition. Compared with 15 °C, the soil CO_2 emission rate increased by 134.2%, 74.1%, and 90.6% on average for 1, 3, and 30 d at 25 °C and decreased by 27.7% and 20.8% on average for 7 and 15 d of incubation, respectively. Meanwhile, the soil CO_2 emission rate increased by 301.8%, 92.4%, and 71.2% at 1, 3, and 30 d of incubation at 35 °C and decreased by 29.6% and 4.0% at 7 and 15 d, respectively.

At 1 and 3 d of straw decomposition, the soil CO_2 emission rate in the organic substitution applications was higher than that of the CF application. At 7 d of straw decomposition, the soil CO_2 emission rates of the CM treatment and straw application were higher and lower than those of the CF, respectively. There were no significant effects on soil CO_2 emission rates under fertilization treatments at 15 and 30 d of straw decomposition. Compared with the CF, the soil CO_2 emission rate in the organic substitution treatments increased by

120.5% and 15.7% on average at 1 and 3 d of straw decomposition, respectively. Meanwhile, the soil CO_2 emission rate of the CM treatment increased by 8.9% on average, and the straw applications decreased by 25.3% on average at 7 d of straw decomposition. The soil CO_2 emission rate showed an overall decreasing trend as straw decomposition advanced. Compared with 1 d of straw decomposition, the soil CO_2 emission rates at 3, 7, 15, and 30 d of straw decomposition decreased by 69.2%, 85.4%, 91.6%, and 95.4% on average, respectively.

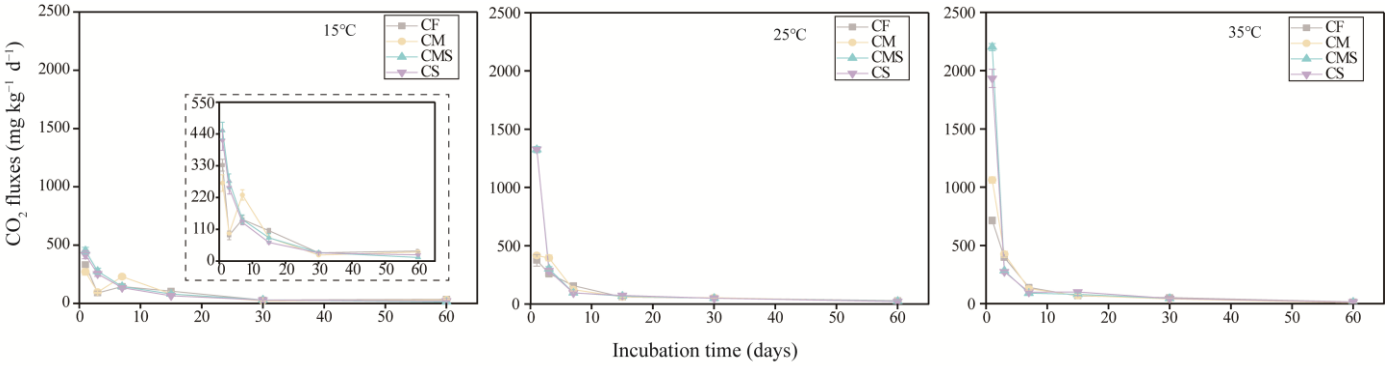

Figure 3. Soil carbon dioxide (CO_2) emission fluxes during straw decomposition under different fertilization treatments and incubation temperatures.

The soil CO_2 cumulative emissions showed an increasing trend with increasing temperature under different fertilization treatments (Figure 4). Compared to 15 °C, the soil CO_2 cumulative emissions increased by 13.8–46.5% and 31.1–72.0% at 25 °C and 35 °C, respectively. Compared to the CF treatment, the organic substitution treatments at 25 °C and 35 °C increased the soil CO_2 cumulative emissions by 5.2–25.7% and 4.7–29.7%, respectively, with the straw applications (CMS and CS) increasing emissions by 24.8–25.7% and 27.1–29.8%, respectively.

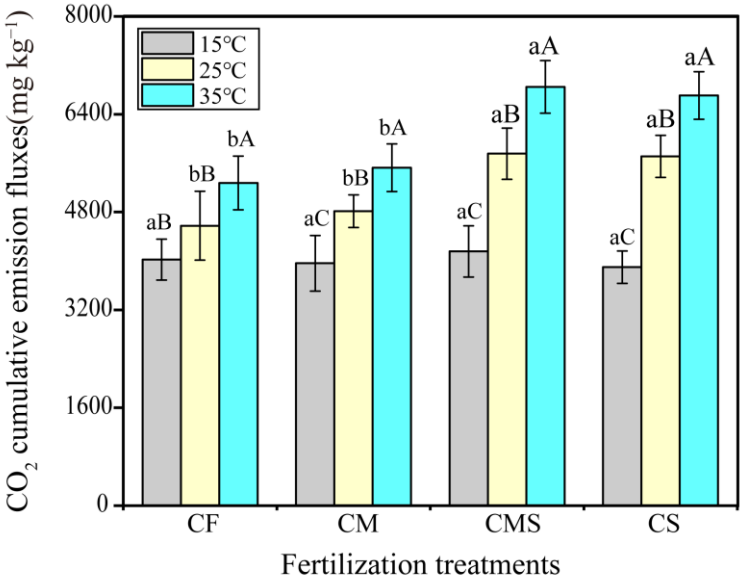

Figure 4. Soil carbon dioxide (CO_2) cumulative emission fluxes during straw decomposition under different fertilization treatments and incubation temperatures. Different lowercase letters indicate significant differences among the different fertilization treatments under the same temperature condition (Duncan test, $p < 0.05$). Different uppercase letters indicate significant differences among the different temperatures under the same fertilization treatment (Duncan test, $p < 0.05$).

3.4. Temperature Sensitivity of Soil CO_2 Cumulative Emissions during Straw Decomposition

During straw decomposition, soil CO_2 cumulative emissions were sensitive to incubation temperature ($Q_{10} \geq 1$) for each fertilization treatment, with more significant effects in the medium temperature range (15–25 °C) for straw application (CMS and CS) (Figure 5). Compared to the CF treatment, the organic substitutions increased the value of Q_{10} by 6.7–28.2%, and straw applications (CMS and CS) increased it by 21.1–28.2% in the medium temperature range. The sensitivity of soil CO_2 cumulative emissions to temperature in the medium temperature range was stronger than that in the higher temperature range (25–35 °C) for each fertilization treatment.

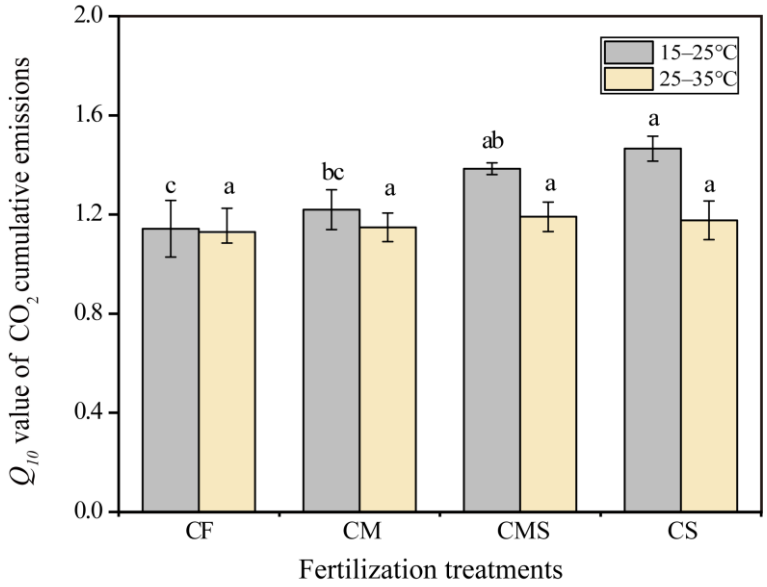

Figure 5. Temperature sensitivity (Q_{10}) of carbon dioxide (CO_2) cumulative emission fluxes under different fertilization treatments and different incubation temperature ranges. Different lowercase letters indicate significant differences among the different fertilization treatments (Duncan test, $p < 0.05$).

3.5. The Relationships among Incubation Temperatures, Fertilization Treatments, Soil Physicochemical Properties, Enzyme Activities, and CO_2 Emissions

As shown in Table 3, the soil EEAs and CO_2 emissions were significantly affected by the incubation temperatures and fertilization treatments, and the effects were varied with incubation periods, with the F values of the incubation periods and incubation temperatures being higher than those of the fertilization treatments. The soil βG, CBH, XYL, NAG, and LAM were significantly affected by the two-by-two interaction of incubation period, incubation temperature, and fertilization treatment through two-way interaction analysis. The interaction between the incubation period and fertilization treatment had a significant effect on soil αG. Soil CO_2 emissions were significantly affected by the interactions of incubation periods with incubation temperatures and incubation periods with fertilization. The interaction between incubation periods, incubation temperatures, and fertilization treatments had significant effects on soil CBH, XYL, NAG, LAM, and αG.

PLS-PM was conducted to investigate the effects of fertilization treatment and temperature on soil physicochemical properties, EEAs, and soil CO_2 emissions (Figure 6). Fertilization treatment (0.86 ***) and temperature (0.05 *) had significant and positive effects on soil physicochemical properties. Furthermore, soil physicochemical properties positively regulated soil CO_2 emissions (0.48 **) and negatively regulated EEAs (−0.45 *). Meanwhile, fertilization treatment (0.65 **) and temperature (−0.58 ***) had significant positive or negative effects on soil EEAs. Soil EEAs negatively regulated soil CO_2 emissions (−0.63 ***). The results showed that fertilization treatments indirectly affect CO_2 emissions by influencing soil physicochemical properties and EEAs. Temperatures affect CO_2 emissions both directly

and indirectly by influencing soil physicochemical properties and EEAs. Interestingly, the effect of temperature on CO_2 emissions was stronger than that of fertilization.

Table 3. Three-way ANOVA for the effects of incubation temperature, fertilization treatment, and incubation period on soil EEAs and CO_2 emissions during straw decomposition (soil EEAs n = 144; CO_2 emissions n = 216).

Factors	βG	CBH	XYL	NAG	αG	LAM	CO_2 Fluxes
Incubation days (Day)	465.5 ***	316.8 ***	645.8 ***	191.7 ***	403.3 ***	757.4 ***	91.0 ***
Fertilization patterns (Fer)	157.4 ***	118.5 ***	158.0 ***	52.3 ***	23.2 ***	34.6 ***	5.3 **
Temperatures (Temp)	588.1 ***	520.8 ***	1384.5 ***	182.1 ***	315.1 ***	275.1 ***	7.2 **
Day × Fer	3.0 *	6.7 ***	6.8 ***	9.9 ***	2.2	21.8 ***	6.5 ***
Day × Temp	57.5 ***	48.6 ***	102.7 ***	50.9 ***	27.5 ***	35.2 ***	5.4 ***
Fer × Temp	3.4 *	12.6 ***	19.0 ***	9.3 ***	1.5	5.5 ***	0.4
Day × Fer × Temp	2.1	5.2 ***	5.7 ***	6.4 ***	3.3 ***	8.2 ***	0.8

Note: βG, β-glucosidase; CBH, β-cellobiosidase; NAG, N-acetyl-glucosaminidase; XYL, β-xylosidase; αG, α-glucosidase; LAM, leucine-aminopeptidase. Duncan test, * $p < 0.01$, ** $p < 0.001$, *** $p < 0.0001$.

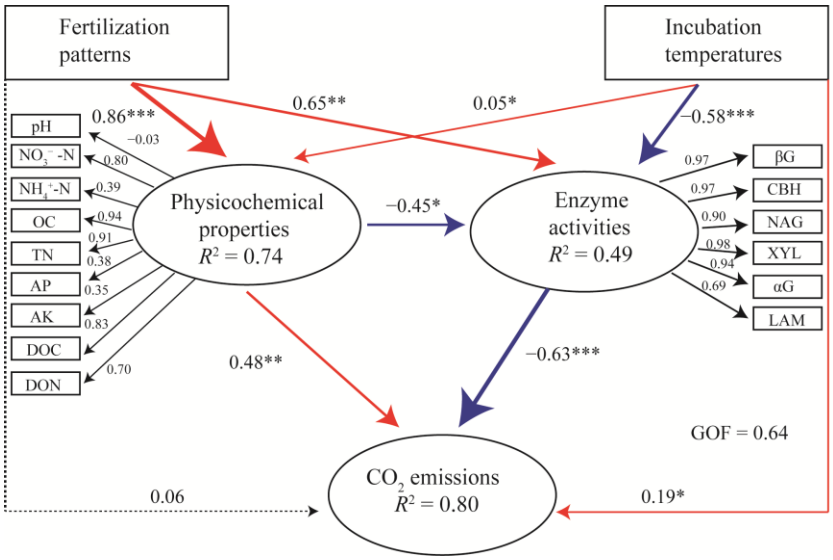

Figure 6. The partial least squares path model (PLS-PM) exploring the direct and indirect effects of fertilization treatments and incubation temperatures on soil physicochemical properties, enzyme activities, and soil CO_2 emissions. Red and blue arrows indicate positive and negative relationships, respectively. Dashed arrows indicate nonsignificant effects ($p > 0.05$). The R^2 value associated with response variables represents the proportion of variance explained by relationships with other variables in the modeling. The goodness-of-fit (GOF) value was calculated to evaluate the model. Square boxes represent variables included in the modeling: OC, organic C; NO_3^--N, nitrate nitrogen; NH_4^+-N, ammonium nitrogen; AP, available phosphorus; AK, available potassium; DOC, dissolved organic C; DON, dissolved organic N; βG, β-glucosidase; CBH, β-cellobiosidase; NAG, N-acetyl-glucosaminidase; XYL, β-xylosidase; αG, α-glucosidase; LAM, leucine-aminopeptidase. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

4. Discussion

4.1. Effects of Fertilization Treatments on Straw Decomposition

Long-term fertilization with organic fertilizer or straw improves the soil microbial community structure composition and increases the EEAs associated with soil carbon and nitrogen cycling, which influence straw decomposition [1,38]. Previous studies have indicated that organic substitutions increase the soil EEAs involved in organic carbon and nitrogen mineralization, e.g., soil βG, CBH, and XYL activities [39,40]. These series of soil EEAs may respond differently to the addition of straw in the different fertilization

treatments. Fan et al. [41] and Wu et al. [42] used incubation experiments with straw additions and indicated that organic substitutions increased soil βG and CBH activities, enhanced straw-C mineralization, and thus accelerated straw decomposition. However, Xiao et al. [43] used incubation experiments with straw additions and found that compared to chemical fertilizer application, the organic substitutions decreased the soil βG, CBH, and NAG activities during the pre-decomposition period of straw. Our results indicated that organic substitutions increased the EEAs (βG, CBH, NAG, and XYL) associated with soil carbon degradation, and the soil EEAs showed a decreasing trend over time as straw decomposed. The reason for these results could be that straw application has a priming effect on the soil, leading to the secretion of enzymes by soil microorganisms for straw C mineralization [44,45]. Long-term organic fertilizer or straw inputs bring a large amount of carbon source material to the soil, and the organic substitution fertilization forms a unique community structure of soil microorganisms that preferentially use fresh C sources and thus secrete hydrolytic enzymes associated with carbon degradation (e.g., cellulose hydrolases) to accelerate straw C turnover and reduce straw C residues [46]. Therefore, organic substitution fertilization has higher carbon-degrading enzymatic activity. Meanwhile, carbon decomposition in straw was faster than nitrogen decomposition, and the EEAs associated with carbon decomposition (βG, CBH, NAG, and XYL) showed an overall decreasing trend with increasing incubation time, while the EEAs associated with nitrogen decomposition (LAM) showed an increasing trend followed by a decreasing one.

Organic substitutions have a positive effect on straw decomposition, which can be expressed as an increase in soil CO_2 emissions [47]. Liu et al. [48] indicated that straw application increases soil active carbon content, organic carbon accumulation, and soil CO_2 emissions by meta-analysis. The results of the incubation experiments based on soil samples from the location experiments with different fertilization treatments showed that soil CO_2 emissions showed a decreasing trend with increasing incubation time, and the organic substitution treatments, especially straw application treatments, were higher than the chemical fertilizer application treatment during the pre-decomposition period of straw [41,42,49]. Our study partially agreed with these findings in that the organic substitution treatments increased soil CO_2 emission rates at 1 and 3 d of straw decomposition compared to chemical fertilizer application. Further, our study found that chemical fertilizer combined with manure and straw (CMS) could increase soil CO_2 cumulative emissions and soil organic carbon mineralization rates compared with chemical fertilizer application. Straw addition has an excitation effect on the soil, leading to increased soil microbial activity and enhanced respiration, and assimilating straw C and producing CO_2 emissions [44,45]. Compared to chemical fertilizer application, the organic substitutions resulted in a relatively nutrient-rich environment with high soil microorganism activity and a rapid rate of straw decomposition, causing a rapid increase in CO_2 emissions in the short term. Our previous studies confirmed that long-term organic substitution treatments, especially straw application treatments (CMS and CS), significantly increased soil EEAs compared to chemical fertilizer application [7,30]. Therefore, in this study, straw decomposition was fastest in the straw addition treatments (CMS and CS) with higher soil organic carbon mineralization.

4.2. Effects of Incubation Temperatures on Straw Decomposition

The decomposition of crop straw is influenced by a combination of soil properties, climatic factors, and straw characteristics [8,9], especially abiotic factors such as soil temperature [10,50]. The process of straw decomposition is accompanied by changes in soil EEAs, and when the temperature changes, soil EEAs change accordingly, which in turn promotes or inhibits the decomposition of soil nutrients and organic matter, affecting the material and energy cycles of terrestrial ecosystems [16,51]. The results of previous studies showed that cellulase activity was inhibited at lower temperatures (<10 °C), but increasing the temperature within a certain threshold could increase the enzyme kinetic constant and thus improve soil EEAs [52]. Souza et al. [53] indicated that increasing temperatures changed

the balance of soil C and N cycles and increased soil βG and XYL activities. In addition, Chen et al. [23], through a meta-analysis, indicated that elevated temperature significantly increased ligninolytic enzyme activity but had no significant effect on cellulolytic enzyme (βG, XYL, and CBH) activities. Qi et al. [54] used incubation experiments with straw additions and found that soil EEAs (βG, CBH, NAG, XYL, αG, and LAM) were higher at 15 °C and 25 °C than at 35 °C. The results of the above studies had inconsistent results regarding the effect of temperature on soil EEAs during straw decomposition. Our results showed that soil CBH, XYL, and αG activities during straw decomposition (7, 15, 30, and 60 d) showed a decreasing trend with increasing temperature, and the same trend was observed for soil βG activities at 7, 15, and 30 d of straw decomposition (Figure 1). The increase in temperature, which accelerates unstable C decomposition with increasing temperature, decreases substrate availability and consequently decreases soil EEAs [15,55,56]. Soil carbon mineralization at 25 °C and 35 °C reached a maximum at 1 d and then decreased rapidly, whereas soil organic carbon mineralization at 15 °C was a slow process (Figure 3), yet soil enzymes were always active. Therefore, soil EEAs were higher at 15 °C than at 25 °C and 35 °C. In addition, our results also found that soil enzymes at different incubation temperatures and fertilization treatments at 7, 15, and 30 d of straw decomposition could be divided into two groups, one at 15 °C and the other at 25 °C and 35 °C, while there was no clear distinction between fertilization treatments (Figure 2). This indicates that the response of soil EEAs to temperature during the main period of straw decomposition was stronger than that of fertilization. The results of the PLS-PM and the three-factor ANOVA also reflected a stronger effect of temperature on the straw decomposition process than the fertilization treatment (Table 3 and Figure 6).

Increasing temperature accelerates carbon utilization by microbes, which in turn increases soil CO_2 emissions due to possible physiological changes in several microbes [57]. Previous studies have indicated that soil CO_2 emissions during straw decomposition show an increasing trend with increasing temperature [58,59], and our results partially agreed with these findings. As shown in Figure 4, soil CO_2 cumulative emissions during straw decomposition showed an increasing trend with increasing temperature. Meanwhile, our results found that soil CO_2 emission rates were higher at 25 °C and 35 °C than at 15 °C at 1 and 3 d of straw decomposition, and the opposite was true at 7 d (Figure 3). The reason for this result may be that the priming effect is weak and lengthy at low temperatures and strong and short at high temperatures, resulting in rapid emissions in the early stage and slow emissions in the late stage at high temperatures. Higher temperatures affect soil microbial community composition and consequently enhance microbial physiological functions (e.g., breathing) [60]. The soil CO_2 emission rate in the straw application tended to decrease over time at each incubation temperature, and the same trend was observed in the chemical fertilizer and organic fertilizer application treatments at 25 °C and 35 °C, but a secondary peak was observed at 15 °C at 7 d in the chemical fertilizer and organic fertilizer applications. This indicates that the soil microorganisms in the straw addition treatments were highly adapted to temperature, while the treatments without straw addition took longer to activate dormant microorganisms at low temperatures [10]. This result confirmed our hypothesis that although the long-term organic substitution treatments failed to resist temperature variation, the long-term straw addition treatments were better adapted to temperature than treatments without straw.

5. Conclusions

The soil CBH, XYL, and αG activities showed a decreasing trend with increasing temperature during straw decomposition, and the same trend was observed for soil βG activity in the first and middle stages of straw decomposition and for NAG and LAM activities in the middle and late stages of straw decomposition. The organic substitutions increased soil βG, CBH, NAG, and XYL activities during straw decomposition, with soil αG activity increasing in the middle and late stages of straw decomposition, soil LAM

activity decreasing in the middle stage of straw decomposition, and soil βG, CBH, and XYL activities being higher in the straw application treatment than in the manure treatment.

The soil CO_2 emission rate at each incubation temperature was the highest on the 1st day of straw decomposition, then rapidly declined until 7 d at 25 °C and 35 °C, slowly declined until 30 d at 15 °C, and remained stable thereafter. Soil CO_2 cumulative emissions tended to increase with increasing temperature under different fertilization treatments. Soil CO_2 cumulative emission fluxes were more sensitive to temperatures in the medium temperature range than in the higher temperature range. Both fertilization treatment and incubation temperature can affect soil CO_2 emissions by influencing soil physicochemical properties and soil EEAs, among which incubation temperature can also directly affect soil CO_2 emissions. Incubation temperature had a stronger effect on the straw decomposition process than fertilization. By examining the effect of fertilization on the straw decomposition process under different incubation temperatures, it was observed that the straw application treatments (CMS and CS) were more suitable to temperature changes.

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