Effects of High Soil Temperature Stress on Microorganisms Utilizing Different Carbon Sources in the Rhizosphere of Pepper Seedlings

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Abstract [**Objectives**] To explore the effects of high soil temperature stress on microorganisms utilizing different carbon sources in the rhizosphere of pepper seedlings. [**Methods**] Using seedlings of the main pepper cultivar 'Reyin 1' as experimental materials, five soil temperature gradients (25, 30, 35, 40, and 45 ℃) were established. After a 96 d cultivation, soil nutrient content and soil microbial functional diversity were measured to elucidate the impact of high soil temperature on the soil microenvironment. [**Results**] As soil temperature increased, the contents of total nitrogen, alkaline hydrolyzable nitrogen, available phosphorus, and rapidly available potassium generally showed a decreasing trend. However, under the 45 ℃ treatment, the contents of total nitrogen, available phosphorus, and rapidly available potassium were the highest among all treatments, although the alkaline hydrolyzable nitrogen content was significantly lower compared to the other treatments. BIOLOG analysis revealed that with increasing soil temperature, the average soil microbial absorbance value and the Shannon diversity index decreased significantly. In contrast, the Shannon evenness index and the Simpson dominance index showed no significant differences across the different temperature treatments. This indicates that as soil temperature rises, the carbon source utilization capacity of the soil microbial community decreases, leading to reduced overall carbon metabolic activity and microbial functional diversity, while the dominant microbial populations remained unchanged during this process. Principal component analysis further confirmed effective separation among the different temperature treatments, suggesting that high soil stress significantly altered the structure of the soil microbial community. [**Conclusions**] In practical production, appropriate measures should be taken to decrease soil temperature to create a favorable rhizosphere microenvironment and thereby promote crop growth.

Key words Pepper, Soil temperature, Soil microorganisms, BIOLOG, Soil microenvironment

0 Introduction

Climate change, characterized by global warming, has garnered significant global attention[1]. In agricultural and forestry production, numerous early studies focused on the impacts of rising temperatures on plant growth[2-3], yield[4-5], and underlying response mechanisms[6-8]. However, as understanding has deepened regarding the threats posed by climate-induced topsoil warming, research has increasingly shifted toward investigating its effects on biodiversity, ecosystems[9], and nutrient cycles of carbon, nitrogen, and phosphorus across different scales[10].

The plant rhizosphere serves as the primary interface between plant roots and the surrounding soil[11], and represents the most active site for soil material cycling and energy flow[12]. In the rhizosphere environment, soil microorganisms act as decomposers of organic materials, such as root exudates and plant litter, and participate in the breakdown and transformation of these substances[13]. This microbial activity drives the release and fixation of nutrients, thereby playing a crucial role in rhizosphere processes[14].

Pepper, a typical tropical crop, is widely cultivated throughout tropical regions of Asia, Africa, and Latin America[15]. In China, it is primarily grown in intensive monoculture systems. To prevent diseases, a common practice is to maintain clean and tidy fields with efficient drainage[16]. However, this practice can lead to a significant increase in soil temperature during the dry season, adversely affecting pepper plant growth. Despite this, research on the effects of such elevated temperatures on the soil microenvironment, particularly on soil microorganisms, remains relatively limited.

As an analytical method for characterizing microbial communities based on carbon source metabolism, the BIOLOG microplate method can classify soil microorganisms according to differences in their carbon metabolism. Compared with other methods such as phospholipid fatty acid (PLFA) analysis, PCR-DGGE, and high-

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throughput 454 sequencing, it is simpler, faster, and more cost-effective. As a result, it is widely used in assessing the functional diversity of soil microbial communities[17-18]. In this study, pepper seedlings were used as the test material in laboratory pot experiments under different temperature gradients. The BIOLOG microplate method was applied to investigate the effects of high soil temperature stress on soil microorganisms. Based on the results, the influence of high soil temperature stress on the soil micro-environment was further elucidated. This research provides a theoretical foundation for understanding the mechanisms underlying soil high temperature stress and for developing corresponding stress mitigation techniques.

1 Materials and methods

1.1 Materials Seedlings were cultivated using the dominant cultivar 'Reyin 1' pepper seeds. After 60 d, uniform pepper seedlings at the three-leaf stage were selected for potting. Once the plants had acclimated, they were subjected to experimental treatments with different soil temperatures.

1.2 Methods

1.2.1 Test treatment. The test soil was a mixture of sand, loam, and coconut coir. The experiment included five treatments: 25 (CK), 30, 35, 40, and 45 ℃. After transplanting and seedling recovery, the pots were transferred to water baths to apply the temperature treatments, each lasting 12 h. Each treatment was replicated 12 times, with 500 g of soil per pot. One uniformly grown pepper seedling was planted in each pot and placed into the water bath. Daily watering maintained soil moisture at approximately 25%, which is suitable for pepper growth, and other routine management practices were followed. The pot experiment was conducted from 2019 to 2020 at the Hainan Provincial Key Laboratory of Genetic Improvement and Quality Regulation for Tropical Spice and Beverage Crops. Heating was applied via water baths to transfer heat to the pots, thereby creating different soil temperature conditions: 25 (control), 30, 35, 40, and 45 ℃. After 96 d of cultivation, functional diversity of soil microbial communities was analyzed using BIOLOG EcoPlates™.

1.2.2 Test indicators and methods. (i) Soil physicochemical properties were determined using conventional methods[19], as specified below: alkaline hydrolysis diffusion was used for available nitrogen; ammonium fluoride-hydrochloric acid extraction (0.03 mol/L NH_4F-0.025 mol/L HCl) followed by molybdenum-antimony anti-colorimetry for available phosphorus; and neutral ammonium acetate extraction followed by flame photometry for available potassium.

(ii) Determination of functional diversity of soil microbial communities. The BIOLOG EcoPlate™ was used for the measurement. Moist soil equivalent to 10.00 g of oven-dried mass was weighed into a 250 mL Erlenmeyer flask, and 90 mL of sterile deionized water was added. The mixture was shaken thoroughly at 4 ℃ for 1 h allowed to stand for 3 min, and then diluted with sterile deionized water to prepare a 10^{-3} soil suspension. Using an 8-channel pipette, 150 μL of this soil suspension was transferred into the wells of the ECO plate. The absorbance at 590 nm was measured every 24 h until the readings stabilized, which generally required incubation for 240 h.

(iii) Data processing and statistical analysis. The absorbance value of each well was used to calculate the Average Well Color Development (AWCD). Diversity indicators, including the Shannon index, Shannon evenness, and Simpson index, were calculated using the absorbance values from the 96-h incubation period. Specific calculation methods referred to Yang Yonghua *et al.*[20] and Zhang Zhiming *et al.*[21]. After calculating the values, one-way analysis of variance (ANOVA) was used to analyze significant differences among different planting years. Principal component analysis (PCA) was performed using the absorbance values of each well at 96 h. Both the one-way ANOVA and PCA were conducted using SPSS 19.0 software.

2 Results and analysis

2.1 Effects of soil high temperature stress on soil nutrient content of pepper Table 1 shows that soil total nitrogen, available nitrogen, available phosphorus, and available potassium generally decreased with increasing temperature. The exception was the 45 ℃ treatment, which resulted in the highest levels of total nitrogen, available phosphorus, and available potassium across all treatments, although its available nitrogen content was significantly lower than the others.

Table 1 Soil nutrient content of different soil high temperature stress treatment

Treatment	TN//%	Alkali-hydrolyzable nitrogen//mg/kg	AP//mg/kg	AP//mg/kg
CK	0.294 ± 0.002 3 bc	33.37 ± 0.70 b	17.27 ± 0.49 ab	154.78 ± 2.84 a
30	0.303 ± 0.001 3 ab	31.97 ± 0.70 b	16.56 ± 0.34 bc	124.81 ± 3.69 b
35	0.288 ± 0.004 1 c	48.77 ± 3.50 a	14.88 ± 0.06 d	110.66 ± 7.00 c
40	0.284 ± 0.001 6 c	31.27 ± 2.80 b	15.59 ± 0.44 cd	115.66 ± 3.60 bc
45	0.310 ± 0.006 0 a	13.07 ± 0.00 c	18.37 ± 0.34 a	159.78 ± 2.84 a

NOTE Data was mean ± standard error; Different letters meant significant difference at $p < 0.05$. The same as below.

2.2 Analysis of carbon source utilization ability of soil microbial community AWCD is an important indicator to characterize the ability of soil microbial communities to utilize carbon sources and reflect the overall activity of carbon metabolism[15]. As shown in Fig. 1, the average absorbance value gradually reached the maximum at 168 h of culture and tended to be stable, so the

average absorbance value at this time was used for analysis. With the increase of soil temperature, the average absorbance value of soil decreased gradually, and the AWCD of the control treatment at 25 ℃ was the highest, followed by the treatment at 30 ℃, but there was no significant difference between them; The AWCD of 45 ℃ treatment was the lowest and significantly lower than that of other treatments. The above results indicated that the carbon source utilization ability of soil microbial community decreased with the increase of soil temperature, and the overall carbon metabolism activity decreased.

2.3 Diversity index analysis The functional diversity indices and evenness of soil microbial communities under different planting years were calculated using the plate well absorbance values after 168 h of incubation. As shown in Table 2, both the Shannon and Simpson indices exhibited a decreasing trend with increasing temperature. Compared to the control at 25 ℃, the Shannon index decreased by 1.90%, 4.68%, 9.14%, and 15.23% at 30, 35, 40, and 45 ℃, respectively. No significant difference was observed between the 25 and 30 ℃ treatments, but the values at 35, 40, and 45 ℃ were significantly lower than those at 25 ℃, with significant differences among these treatments as well. Compared to the control, the Shannon evenness decreased by 20.69%, 5.93%, and 47.23% at 30, 35, and 45 ℃, respectively, while it increased by 8.23% at 40 ℃. In addition, the Simpson index decreased by 6.07%, 12.04%, 28.69%, and 49.78% at 30, 35, 40, and 45 ℃, respectively, compared to the control at 25 ℃. These results indicate that both the functional diversity index and Simpson dominance index of soil microbial communities decreased with increasing soil temperature, which is generally consistent with the trend observed in the average absorbance values of soil microbes. This demonstrates that as soil temperature rises, both microbial activity and diversity in the soil tend to decline.

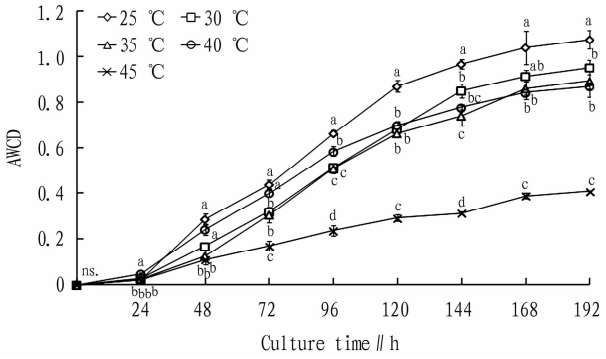

Fig. 1 Effects of soil temperature on the AWCD of pepper soil

Table 2 Effects of soil temperature on soil microbial diversity index of pepper

Treatment	Shannon index	Shannon evenness	Simpson dominance index
CK	3.02 ± 0.04 a	5.05 ± 0.05 ab	0.17 ± 0.01 a
30 ℃	2.96 ± 0.01 ab	4.00 ± 0.12 c	0.16 ± 0.01 ab
35 ℃	2.87 ± 0.04 b	4.75 ± 0.14 b	0.15 ± 0.00 b
40 ℃	2.74 ± 0.05 c	5.46 ± 0.22 a	0.12 ± 0.00 c
45 ℃	2.56 ± 0.06 d	2.66 ± 0.16 d	0.09 ± 0.01 d

2.4 Differences in utilization of different types of carbon sources by soil microorganisms Based on the chemical functional groups, the 31 carbon sources on the ECO plate were divided into 6 categories: carbohydrates and their derivatives, amino acids, carboxylic acids, polymers, phenolic acids, and amines. The absorbance values for each category of carbon sources were averaged before analysis. As shown in Fig. 2, the utilization of different carbon sources by soil microorganisms varied significantly under different soil temperature treatments, indicating that the structure of the soil microbial community changed as soil temperature increased. With the exception of amines, the utilization of other carbon sources by microorganisms gradually decreased as soil temperature rose. Based on the extent of decline, these carbon sources can be divided into two categories. The first category includes carbohydrates and phenolic acids, whose utilization declined relatively evenly with increasing temperature. The second category includes amino acids, carboxylic acids, and polymers, which showed only minor declines at 25, 30, 35, and 40 ℃, but a significant drop at 45 ℃, forming a clear difference. The trend for amine carbon sources differed from the above. At different incubation times, their utilization initially decreased and then increased with rising temperature, thus reaching the lowest point at 35 ℃.

2.5 Principal component analysis of soil microbial community functional diversity Principal component analysis (PCA) was performed using the plate well absorbance values after 168 h of culture. Two principal component factors were extracted, and a loading plot was generated (Fig. 3). The cumulative variance contribution rate of the two principal component factors reached 62.27%, indicating that these two factors effectively explain the majority of the differences among soil samples under different temperature treatments. The variance contribution rate of the first principal component (PC1) was 36.04%, while that of the second principal component (PC2) was 26.23%. On the PC1 axis, the CK and 30 ℃ treatments were distributed in the positive value region, while the other treatments were located in the negative value region. On the PC2 axis, the 40 ℃ treatment was distributed in the positive value region, the 45 ℃ treatment in the negative value region, and the CK, 30 ℃, and 35 ℃ treatments were clustered around the zero point region. Therefore, principal component analysis effectively separated the soil microbial communities under different temperature treatments. The 25 and 30 ℃ treatments were mainly concentrated in the positive value region along the boundary between the first and second quadrants of the loading plot, while the 35 ℃ treatment was distributed in the negative value region along the same boundary. The 45 and 40 ℃ treatments were located in the third and fourth quadrants, respectively. These results further indicate significant changes in the structure of the pepper rhizosphere soil microbial community as soil temperature increased.

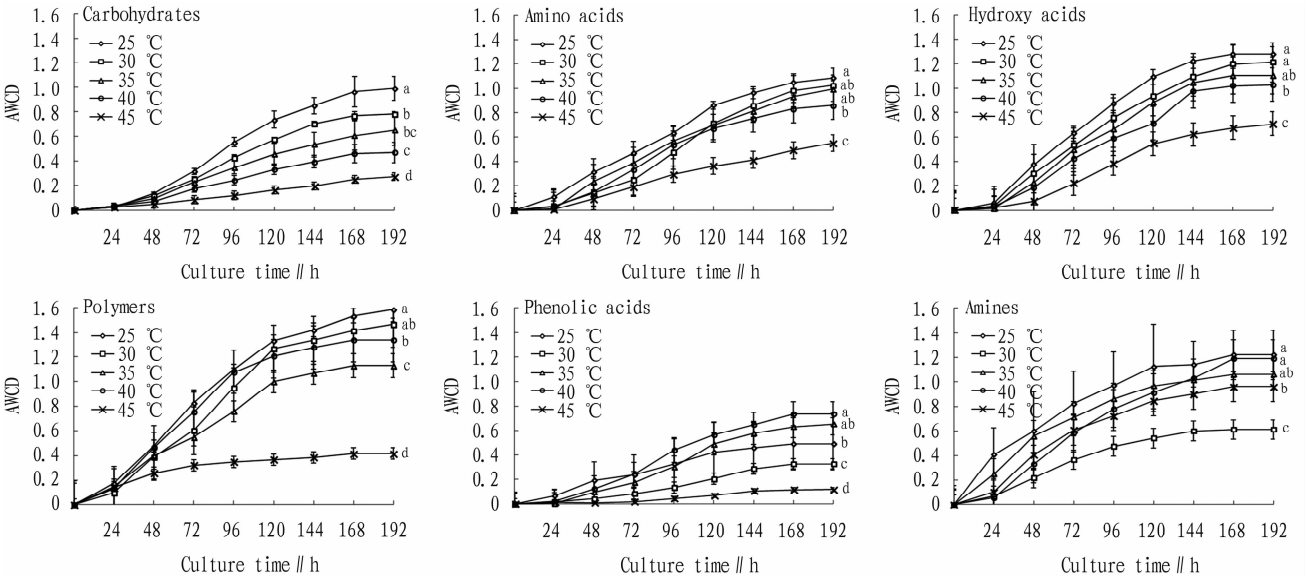

Fig. 2 Utilization of different carbon sources by soil microbe under different temperature stresses

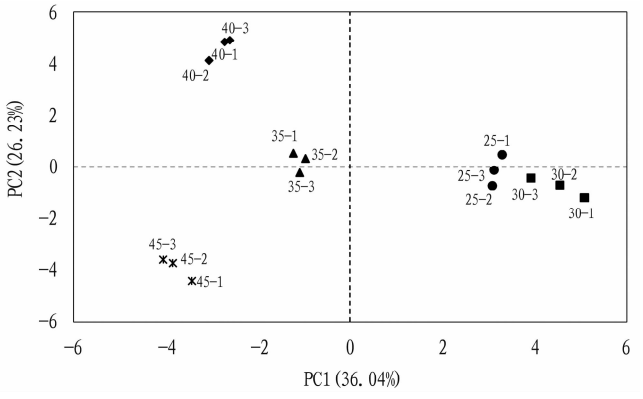

Fig. 3 Principal component analysis of soil microbial communities under different temperature stresses

3 Discussion and analysis

Soil serves as the primary site for plant roots to absorb nutrients, and its nutrient status directly influences the amount of nutrients acquired by plants[14]. While some soil nutrients exist in inorganic forms, the majority are stored in organic forms. Consequently, the decomposition of soil organic matter not only influences the carbon cycle but also accompanies the release and fixation of nutrients such as nitrogen and phosphorus[22]. Microorganisms act as the principal decomposers of soil organic matter, thereby playing a crucial role in the cycling of carbon, nitrogen, and phosphorus, as well as in energy flow within soils[23]. When soil temperature increases, changes in soil microbial biomass and community structure occur, which consequently affect the nutrient cycling processes of carbon, nitrogen, and phosphorus[12].

In this study, with the exception of the 45 ℃ treatment, the contents of alkali-hydrolyzable nitrogen, available phosphorus, and available potassium in the soil generally decreased as soil temperature increased (Table 1). Combined with BIOLOG analysis, the capacity of soil microorganisms to utilize carbon sources was significantly reduced at higher temperatures (Fig. 1), indicating a pronounced decline in microbial activity. This reduction in microbial function consequently impedes the decomposition of organic matter in the soil, thereby disturbing the nutrient cycling of nitrogen, phosphorus, and potassium under elevated temperature conditions. In the 45 ℃ treatment, the soil exhibited the highest levels of total nitrogen, available phosphorus, and available potassium across all treatments, although the content of available nitrogen was significantly lower compared to other groups. This pattern may be attributed to nutrient accumulation in the soil resulting from impaired nutrient uptake by pepper seedlings under high-temperature stress at 45 ℃.

Elevated soil temperature is generally known to reduce the diversity of soil microbial community structure[24]. In this study, the diversity index results indicated that the Shannon diversity of soil microorganisms decreased significantly with increasing soil temperature, whereas the Shannon evenness index and Simpson dominance index showed no significant differences across temperature treatments. This pattern can be explained by the fact that different indices reflect distinct aspects of diversity: the Shannon index and Shannon evenness primarily indicate species richness and the uniformity of species distribution, while the Simpson index reflects the dominance of the most abundant species in the community[17,25].

Therefore, the findings of this study indicate that although microbial diversity decreased with rising temperature, the dominant microbial populations remained largely unchanged throughout this process. Analysis of variations in carbon source utilization among microbial groups under different soil temperatures (Fig. 2) further revealed that microorganisms utilizing amino acids, carboxylic acids, and polymers showed minimal changes with increasing temperature and decreased markedly only at 45 ℃. These groups represent the dominant microbial populations in the soil and were relatively less affected by elevated temperatures. In contrast, microorganisms that metabolize carbohydrate and phenolic acid carbon sources exhibited a significant and consistent decline as soil

temperature increased, indicating their higher sensitivity to thermal stress among soil microbial communities. This differential sensitivity directly contributes to the alteration of soil microbial community structure, as reflected in the principal component analysis (Fig. 3).

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