



Addition of cellulose degrading bacterial agents promoting keystone fungal-mediated cellulose degradation during aerobic composting: Construction the complex co-degradation system

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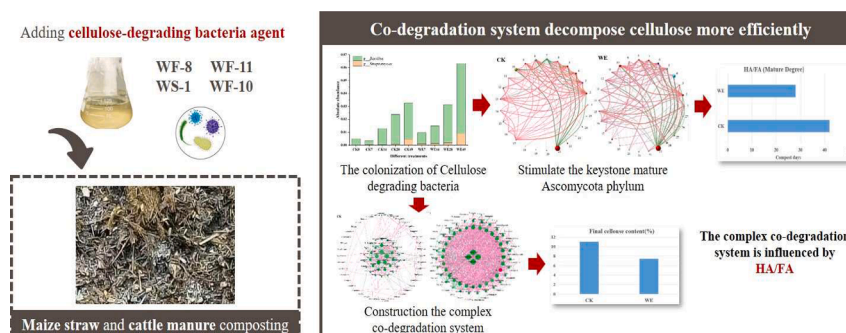
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HIGHLIGHTS

- Cellulose-degrading bacterial and fungal community constitute co-degradation system.
- Keystone decomposing fungi are the foundation of co-degradation systems.
- Cellulose co-degradation system is controlled by C/N and HA/FA of the composting.

GRAPHIC ABSTRACT



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ABSTRACT

To excavate a complex co-degradation system for decomposing cellulose more efficiently, cellulose-degrading bacteria, including *Bacillus subtilis* WF-8, *Bacillus licheniformis* WF-11, *Bacillus Cereus* WS-1 and *Streptomyces Nogalater* WF-10 were added during maize straw and cattle manure aerobic composting. *Bacillus* and *Streptomyces* successfully colonized, which improve cellulose degrading ability. Continuous colonization of cellulose-degrading bacteria can promote the fungi to produce more precursors for humus and promote the negative correlation with Ascomycota. In the current study, the addition of cellulose-degrading bacteria has resulted in the rapid development of *Mycothermus* and *Remersonia* in the phylum Ascomycota as keystone fungal genera which constitute the foundation of the co-degradation system. Network analysis reveals the complex co-degradation

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system of efficient cellulose bacteria and mature fungi to treat cellulose in the process of straw aerobic composting mainly related to the influence of total carbon (TC)/total nitrogen (TN) and humic acid (HA)/fulvic acid (FA). This research offers a complex co-degradation system more efficiently to decompose cellulose aiming to maintain the long-term sustainability of agriculture.

1. Introduction

According to Jia et al. (2018), agricultural production yields 8.19 million tons of straw on a dry weight basis. However, large-scale maize farming generates a considerable amount of straw agricultural waste that is frequently not adequately managed, surpassing the environment's natural carrying capacity and leading to significant environmental pollution and ecological issues (Shen et al., 2005). In terms of the amount of available biomass, maize straw is one of the four major agricultural by-products, with less than 1% of corn stalks collected for industrial processing (Chen et al., 2021). In the context of carbon emission reduction, the most effective use of straw is returning it to the field. Straw returning can maintain the balance of soil carbon pool, improve soil quality, enhance soil fertility, restore and maintain the farmland ecosystem. However, there are some unfavorable phenomena such as slow maturity of straw, competition for nitrogen with crops and aggravation of diseases and insect pests (Floudas et al., 2012). It is usually mixed with dry poultry manure or sewage sludge to obtain the C/N ratio required for composting (Guo et al., 2012). Therefore, the return of bio-rotten straw to the field has become the main way to deal with straw.

Aerobic composting is a technique to decompose large amount of straw, which can promote the degradation of organic matter and formation of humus (Bernal et al., 2009; Tuomela et al., 2000; Wu et al., 2017). However, straw contains a large amount of lignocellulose, which is the primary component of complex plant cell walls. Refractory cellulose has become an important reason to improve the quality of composting (Chen et al., 2021). Several relevant studies have screened and identified microorganisms that enhance the degradation of cellulose, and the application of these specific functional microorganisms to compost can improve the degradation of cellulose (Rastogi et al., 2010; Zhang & Dong, 2022). In this regard, fungi and bacteria have received increasing attention in recent years due to their ability to produce a variety of cellulases. Fungi are the main producers of lignocellulosic enzymes, but bacteria generally have higher growth rates than fungi and their lignocellulosic enzymes are more resistant to high temperatures.

The ability of microorganisms to transform organic materials into compost has become an important factor affecting its quality. Specific cellulose-degrading bacteria can improve the efficiency of cellulose degradation and compost quality (Liu et al., 2022). Previous studies have shown that the addition of exogenously applied microorganisms significantly balances the C/N, improves the utilization efficiency of total sugar, increases the efficiency of cellulose degradation, and increases humus formation during co-composting (Zhao et al., 2022). The reinforcement effect of microbial agents on fungi highly efficient at degrading cellulose accelerates the formation of humic acid and improves the humification rate and compost stability (Wang et al., 2022). Cellulose-degrading bacterial agents not only participate directly in cellulose degradation but also change the bacterial community succession and increase the abundance of bacterial communities related to cellulose degradation, providing more precursors for humus synthesis (Bialobrzeski et al., 2015; Wang et al., 2022).

Microorganisms, including both bacteria and fungi, play crucial roles in composting and affect its maturity (Zhao et al., 2022). Studies have found that fungi play important roles in the degradation of lignin and cellulose (Floudas et al., 2012). Many fungi that can help mature compost are formed during the process of composting. Cellulase spreads continuously during the process of cellulose degradation, promoting the degradation of cellulose and lignin (De Gannes et al., 2013). At each

stage of composting, the fungal community is more stable in resisting environmental changes and plays different roles during the transformation of organic matter into stable humus (Xie et al., 2021).

Previous studies have focused on the ability of bacterial or fungal communities to degrade lignocellulose. However, the current production urgently requires a more efficient complex co-degradation system of cellulose-degrading bacteria and keystone mature fungi communities to deal with lignocellulose. This approach can make full use of an efficient microbial degradation system to deal with lignocellulose.

We hypothesized that (1) there exist a complex co-degradation system of efficient cellulose bacteria and mature fungi to treat cellulose in the process of straw aerobic composting. (2) this complex co-degradation system is activated by cellulose-degrading bacteria and maintained by the keystone fungal community. (3) This complex co-degradation system is mainly controlled by the critical nutrient cycling of the composting.

2. Materials and methods

2.1. Screening and molecular identification of cellulose-degrading bacteria

Four bacterial strains were screened from maize straw and cattle manure composting that could degrade cellulose, including *Bacillus subtilis* WF-8, *Bacillus licheniformis* WF-11, *Bacillus Cereus* WS-1 and *Streptomyces Nogalater* WF-10. The respective bacterial strains were fermented and purified and then preserved at -80°C in 20% glycerol, which preserved in the China strain preservation Center. The strains were then grown on Luria-Bertani (LB) and International Streptomyces Project (ISP2) plates at 30°C . Each bacterial isolate were cultured on the culture medium followed by incubation on an orbital Shaker (Annoron T320, Chinese) at 200 rpm for 3 days at 30°C . The agent was prepared using the cellulose degrading microbial selected.

2.2. Aerobic composting of Cattle manure-maize straw

Cattle manure (CM), maize straw (MS) and cellulose degrading bacteria agent were selected as composting materials. The basic properties of composting materials were as follows: Fresh CM was collected from the Sansheng Animal Husbandry Workstation, located in Misha Town, Dehui City, Jilin Province, China. The CM was stored desiccated without light and dried naturally until the moisture content (MC) reached 50% (Table S1). The MS was taken from the Changchun Mishazi Agricultural Experimental Station, and the MS was crushed into uniform smaller pieces by agricultural grinder (3 cm). The experiment was conducted in the middle universe composting device that was 71 cm long, 51 cm wide, 54 cm tall, and 3.5 cm thick. The composting experiment was divided into two groups. One treatment that contained 50 kg CM and 10 kg MS was evenly blended (CK). Another treatment included contained 50 kg CM and 10 kg MS and 3L of 5% cellulose-degrading bacteria agent (WE). To better promote composting, the initial composting C: N was established to 25–30, and the initial composting moisture was adjusted to 65% using straw and pure water. The stack was turned every five days to ensure that adequate oxygen was supplied, so that the composting was aerobic. Samples were taken at days 0, 7, 14, 21, 28, 35 and 49 of composting. The uniformity of sample was ensured by taking samples from the upper, middle and lower layers of the composting reactor, and the mixed sample was repeated three times (Wang et al., 2022). The samples were stored at -80°C for further

analysis.

2.3. Physicochemical and humification analyses

The physicochemical properties of samples were determined using international standard test methods. The total nitrogen (TN) was assayed using the $\text{H}_2\text{SO}_4\text{-H}_2\text{O}_2$ digestion method determined with a SmartChem2000 (Skalar, Breda, the Netherlands). The dissolved organic matter was analyzed using a total organic carbon analyzer (TOC-L) (Shimadzu, Kyoto, Japan). The total carbon (TC) was determined directly by an element analyzer (Elemental Analyzer System Vario MACRO cube, Elementar, Langensfeld, Germany). The temperature was measured each afternoon through electronic thermometer. The pH and EC were determined by pH and conductivity meters. The above indicator was tested as described elsewhere (Ye et al., 2021). The contents of humic acid (HA) and fulvic acid (FA) were determined by the dinitrosalicylic acid and ninhydrin colorimetric methods, respectively (Cao et al., 2013). The contents of humus and its components were determined by standard measures (Wang et al., 2022).

2.4. High-throughput sequencing

The DNA was extracted using a Fast DNA® Spin Kit for Soil and a Fast Prep® instrument (Catalogue No. 6560–220; MP Biomedicals Germany, Eschwege, Germany) according to the manufacturer's instructions. The V3–V4 variable regions of bacterial 16S rRNA were amplified using the primers 338F (ACTCCTACGGGAGGCAGCA) and 806R (GGACTACHVGGGTWTCTAAT). The PCR products of 16S rRNA gene were sequenced; and sequences were clustered into operational taxonomic units (OTUs) at the 97% threshold. The ITS1 hypervariable region was then amplified by PCR, which utilized the primers ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTCTTCATC-GATGC). A NovaSeq 300 Cycles Kit was used to sequence 2×150 bp paired-end reads using Illumina NovaSeq 6000 (San Diego, CA, USA), following construction of the amplified fungal sub-library. The sequences were clustered into operational taxonomic units (OTUs) at the 97% threshold, and the taxonomic annotation was performed using Mothur against the FUNGuild database ((Nguyen et al., 2016; Tedersoo et al., 2014).

2.5. Statistical analysis

Correlations network analysis was performed with Gephi (version 0.9.2). Non-metric Multidimensional Scaling (NMDS) based on the Bray-Curtis distance were performed to reveal the differences of microbial community between different treatments using the “vegan” package with R (V3.4.2). R (V3.4.2) was used to perform a redundancy analysis (RDA) that aimed to confirm the contribution between cellulose degrading system and maturity change.

3. Result and discussion

3.1. Effect on colonization process of cellulose degrading bacterial agent on co-degrading system

The physicochemical properties and Maturity index of the CM, MS and cellulose degrading bacterial were subjected to aerobic co-composting during 49 days (See supplementary materials). *Bacillus* and *Streptomyces* were successfully colonized, and abundance of WE was higher than CK during each stage of compost (Fig. 1). The visualization of fungal community network interaction was compared with the CK, the negative correlation of fungal network was stronger than the positive correlation (Fig. 2). It clearly showed that phylum Ascomycota dominated the negative correlations which was the core fungal colony related to cellulose decomposition and humus formation. The negative correlation of fungi in compost was enhanced after the addition of

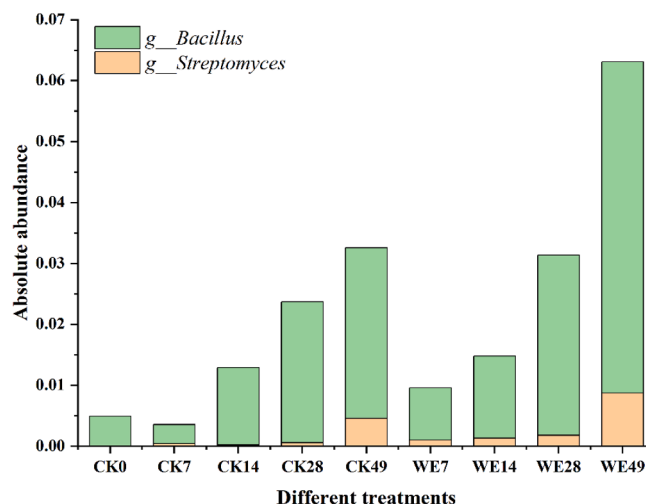


Fig. 1. Colonization of cellulose-degrading bacteria in composting system during different treatments CK: Cattle manure (CM), maize straw (MS) WE: Cattle manure (CM), maize straw (MS) and cellulose-degrading bacteria.

cellulose-degrading bacteria agent (Fig. 2). In this study, all the networks had a negative correlation with Ascomycota, which indicated that the addition of cellulose degrading bacterial agents increased the stability of fungal community (de Vries et al., 2018). There is a complex co-degradation system including cellulose-degrading bacteria and keystone mature Ascomycota community to deal with cellulose together. This complex co-degradation system enhanced the utilization of cellulose. The humic substance (HS) of the CK increased by 19.14%, while that of WE increased by 55.52%. The cellulose content of the CK was 10.41%, and that of the WE was 8.94% (See supplementary materials). The higher HS content in the final compost product in agreement with the enhanced degradation of cellulose (Mao et al., 2020). Generally, ligno-cellulose can be decomposed into polysaccharides, simple sugars and phenolic compounds, which could be the precursors for HS formation (Wu et al., 2017). HA/FA has been widely used to indicate the compost maturity and polymerization degree of HS. A compost is considered to be mature when HA/FA value is above 1.9 (Nigussie et al., 2021). The HA/FA of CK reaches maturity at 42 days, while that of the WE reach maturity at 28 days (See supplementary materials). Due to the complex co-degradation system formed by the addition of cellulose degrading bacteria, WE treatment got maturity much faster than CK.

3.2. Effects of cellulose degrading bacterial agent on the keystone fungal community composition

Changes in the fungal community composition after inoculation with cellulose degrading bacterial agent were evaluated by comparing the WE with CK in the top 10 phylum and genes (Fig. 3). Ascomycota, Basidiomycota, Mortierellomycota, Chytridiomycota and Glomeromycota constituted the major fungal phylum, while Ascomycota occupied more than 80% of the fungi at 14–35 days. *Mycothermus* and *Remersonia* had become the primary fungal genes after 14 days of composting, and both are members of Ascomycota. NMDS analysis was performed on the fungal community structure in the CK and WE treatments based on the OTU level (Fig. 4). A PERMANOVA analysis was used to identify the effect of addition of cellulose degrading bacterial agent on the fungal community. The fungal community structure under the WE treatment ($R^2 = 0.51$, $P = 0.001$, Stress = 0.1199) was more affected compared with the CK treatment ($R^2 = 0.38$, $P = 0.001$, Stress = 0.1675). The oligosaccharides and monosaccharides produced by cellulose degrading are important precursors for the synthesis of humus. When a microbial community is changed by the addition of exogenous microorganisms, its physiological and metabolic functions will also

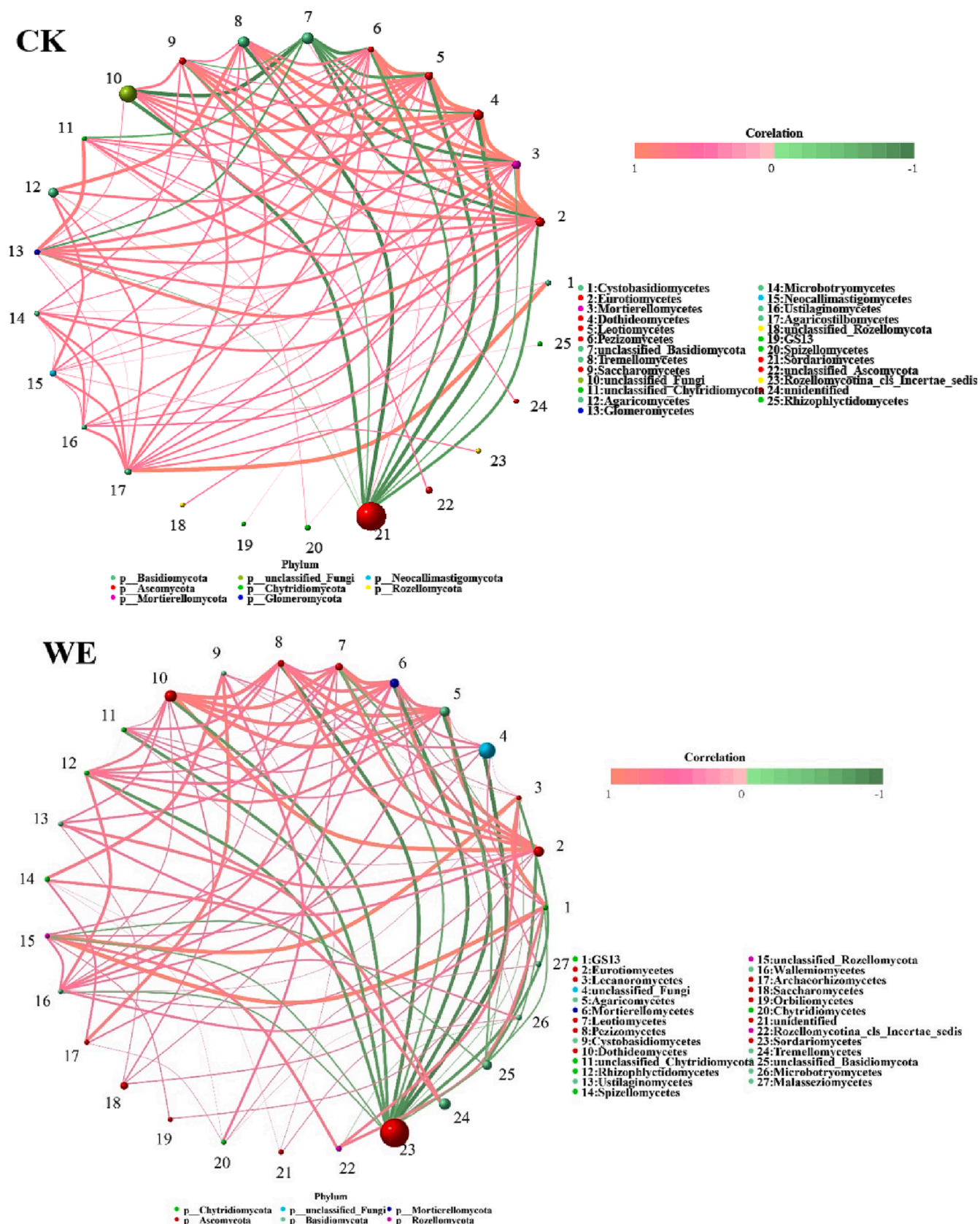


Fig. 2. Differences of Pearson correlation network during each group. Red line means positive correlation, green line means negative correlation. CK: Cattle manure (CM), maize straw (MS) WE: Cattle manure (CM), maize straw (MS) and cellulose-degrading bacteria.

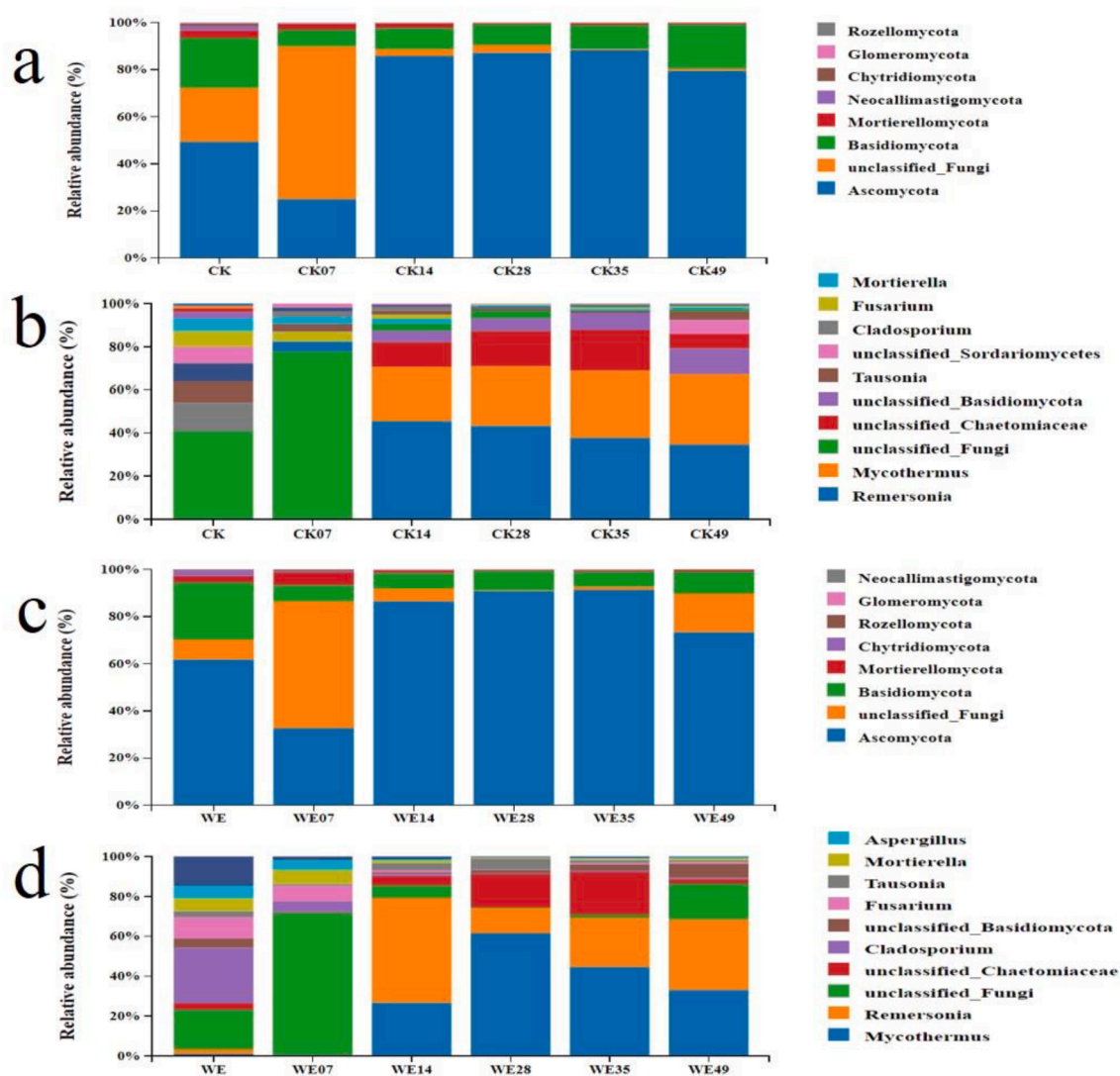


Fig. 3. Effect of the addition of bacteria that degrade cellulose on the composition of fungal phylum and genus (a & b), CK: Cattle manure (CM), maize straw (MS) (c & d), WE: Cattle manure (CM), maize straw (MS) and cellulose-degrading bacteria.

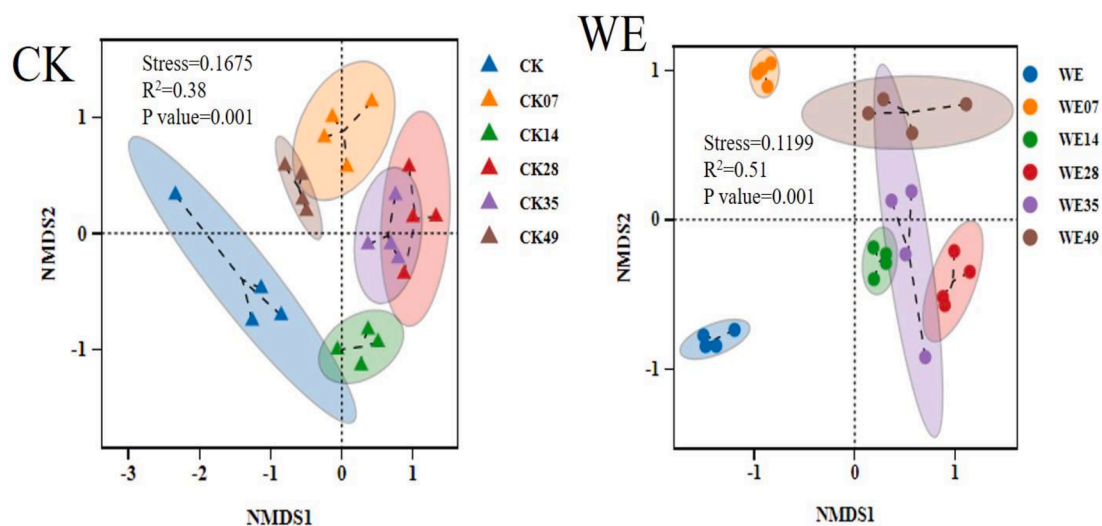


Fig. 4. Non-metric Multidimensional Scaling (NMDS) based on the Bray-Curtis distance of different treatments. CK: Cattle manure (CM), maize straw (MS) WE: Cattle manure (CM), maize straw (MS) and cellulose-degrading bacteria.

change, which will affect the decomposition of cellulose and hemicellulose, and thus, affect the formation of humus (Liu et al., 2018). Its formation involves both the degradation of organic matter and the polymerization of precursors. Lignocellulose is primarily degraded by many functional enzyme during the process of composting. The structure of lignin is destroyed by lignin peroxidase, manganese peroxidase and laccase that produce phenolics (Madadi et al., 2021), which are then

converted into quinones by bacteria. Quinones are concentrated on the humus skeleton, which promotes their synthesis. Fungi play an important role in cellulose degradation because they can produce extracellular enzymes to degrade various polymers, such as cellulose and lignin, and organic matter and can resist drastic changes in the nutrient environment during composting (Liu et al., 2021).

The addition of cellulose degrading bacterial led to more

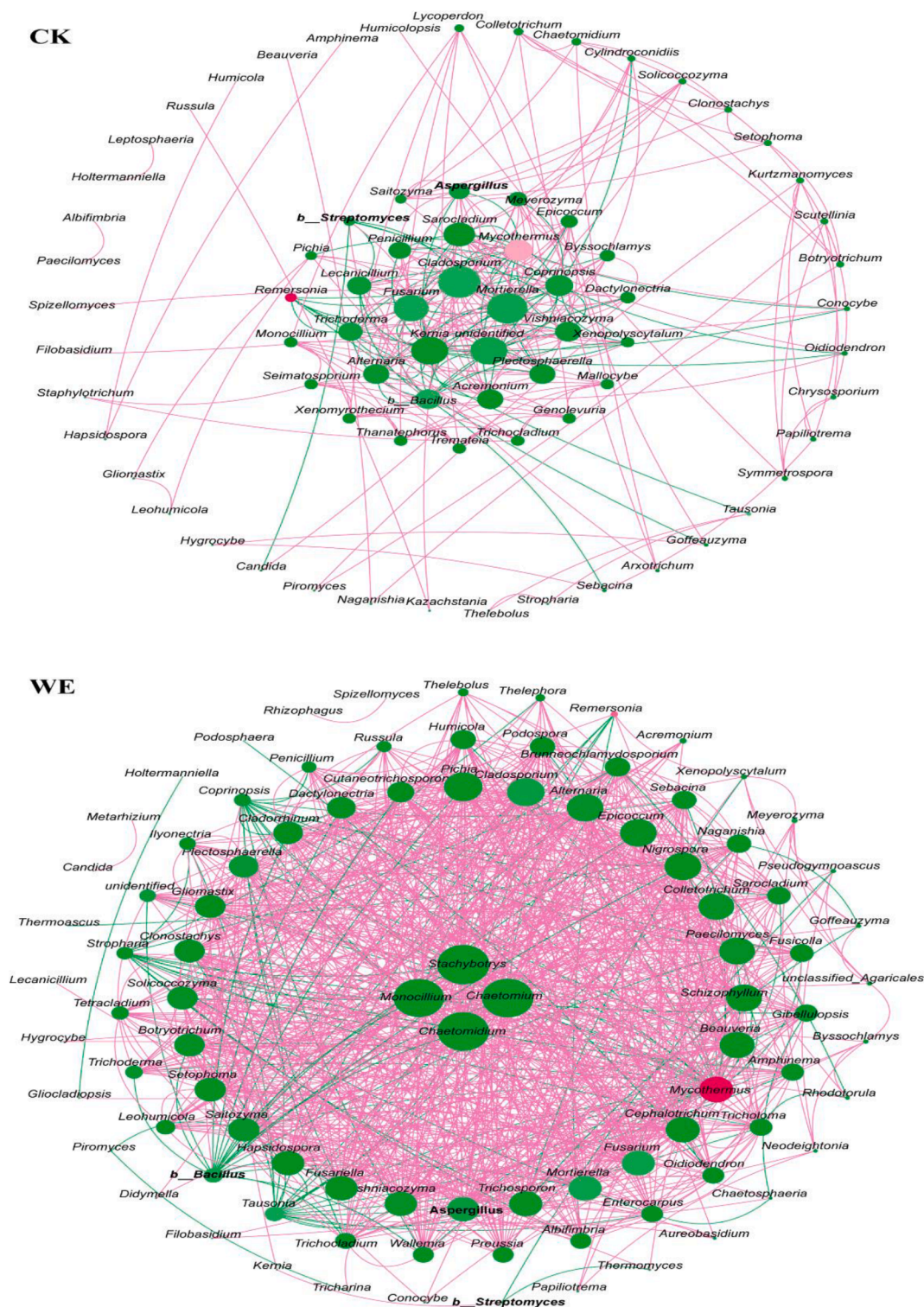


Fig. 5. Differences of keystone microbiome changes of co-occurrence network relationship Cellulose degradation system. Red line means positive correlation, green line means negative correlation. Dot size corresponds to microbiome abundance. CK: Cattle manure (CM), maize straw (MS) WE: Cattle manure (CM), maize straw (MS) and cellulose-degrading bacteria.

concentrated changes in the indigenous fungi in the compost and formation of dominant strains to degrade cellulose. It was shown that the addition of cellulose degrading bacteria improved the activity of specific fungi, which survived for a longer time. Typically, this occurs at the beginning of the aerobic composting, and high temperature inhibits the growth of most fungi (Gu et al., 2017). As the composting process progressed, Ascomycota became the keystone fungi; their abundance increased continuously during the middle temperature and thermophilic periods (Bonito et al., 2010). With the occurrence of cooling and maturation stages, the compost temperature gradually decreased. Many fungi that could have been dormant recovered, and the number of fungal species increased (Lopez-Gonzalez et al., 2015). Ascomycota plays an important role in the decomposition of the heap (Fig. 3), and saprophytic Ascomycota promoted the transformation of straw and manure into humus (Liang et al., 2022). The Ascomycota are closely related to the cellulose-degrading bacteria and keystone mature fungi community as a complex co-degradation system to deal with lignocellulose, which can more quickly utilize and decompose substrates.

3.3. Keystone microbiome changes of cellulose co-degrading system network

The interaction of keystone microbiome plays an important role for degradation of cellulose. A co-occurrence network was constructed using all 226 OTUs of the two treatments to detect keystone co-degradation system (Fig. 5). The network complexity and interaction of bacterial communities revealed by calculating the topological index Degree (Liang et al., 2022). The results showed that the keystone network relationship of WE was more complex than that of CK, and more mature fungi enter into the keystone microbiome. The addition of cellulose-degrading bacterial agents can enhance the interaction of complex keystone microbial degradation system. Generally speaking, from the results of the degree index, the network of WE is the most complex, with 2062 for WE and 544 for CK, which is much larger than that of CK. As illustrated (Fig. 5), the free development of *Bacillus* and *Streptomyces* in CK did not form a dominant cellulose degrading system to specifically decompose cellulose. However, after inoculating cellulose-degrading bacterial agents, *Stachybotrys*, *Monocillium*, *Chaetomium* and *Chaetomium* ect. represented the maturity and cellulose-degrading fungi, which drove other keystone fungal communities belonging to Ascomycota and cellulose-degrading bacteria, which participate in cellulose degrading process. Thus, joint venture of cellulose-degrading bacteria and keystone mature fungal communities as a complex co-degradation system deal with lignocellulose more efficiently.

3.4. Confirming the contribution between cellulose co-degrading system and maturity change

The results of a redundancy analysis (RDA) explained the influence of dramatically changing substances (C/N, HA/FA, cellulose content, temperature, HS, and pH) and the complex co-degradation system during composting. C/N and HA/FA are significant influencing factors, which primarily determine the changes of the complex co-degradation system (Table 1). In the CK, the rate of interpretation of C/N and HA/FA reached 58.2%, and in the WE treatment, the rate of interpretation of C/N and HA/FA reached 66.8%. HA/FA is the first influencing factor, and the influence of HA/FA on the fungal community increased from 35.3% to 41.3% owing to the complex co-degradation system. These results show that the changes in HA/FA and C/N are important factors that affect fungal community, and the rate of HA/FA and C/N that explained the change of co-degradation system increased from 58.2% to 66.8%, respectively. This proved that it intensified the humification process of materials by fungi causing the rapid degradation of cellulose (Qiao et al., 2021). Recent studies have shown that reducing sugars and polysaccharides produced by the degradation of lignocellulose are

Table 1

Main explanatory factors for fungal communities in during aerobic composting. (a) CK: Cattle manure (CM), maize straw (MS). (b) WE: CM, MS and cellulose degradation microbial agent. (* stands for significance * $P < 0.05$, ** $P < 0.01$).

Name	CK			WE		
	Explains %	Total Explains %	P	Explains %	Total Explains %	P
HA/FA	35.3**	35.3	0.003	41.3**	41.3	0.003
C/N	22.9*	58.2	0.038	25.5*	66.8	0.035
Cellulose content	15.6	73.8	0.043	18.0	84.8	0.715
Temperature	10.9	84.7	0.542	5.9	90.7	0.542
HS	8.5	93.2	0.648	5.5	96.2	0.648
pH	6.8	100	0.685	3.8	100	0.685

Note: C/N: Total carbon: Total nitrogen; FA: fulvic acid; HA: humic acid; HS: humic substances.

essential precursors for the formation of humus material, which can be polymerized with amino acids to synthesize humic substances (Wang et al., 2022). Such small molecular weight compounds can also act as nutrients for microorganisms, which leads to a production in precursors and promotes the synthesis of humus (Zhang et al., 2018). This could be closely related to the participation of more microbial precursors in the fungal community of polyphenols and reducing sugars in the Maillard reaction in the humification pathway (Zhou et al., 2022). Therefore, the inoculated microbial agents can promote the bacteria to produce more precursors for humus and promote the keystone fungi to decompose cellulose and increase humus synthesis, which suggests a biotechnological technique.

4. Conclusions

In conclusion, inoculating cellulose-degrading bacteria to stimulate keystone maturity fungi revealed a more efficient complex co-degradation system for dealing with lignocellulose. Continuous colonization of cellulose-degrading bacteria promotes the production of humus precursors, which results in a negative correlation with Ascomycota and ultimately leads to an improvement in the cellulose-degrading ability of keystone maturity fungi. This excavation of the co-degradation system's degradation potential highlights the potential for enhanced decomposition of lignocellulose and underscores the importance of promoting the interaction between cellulose-degrading bacteria and keystone maturity fungi in the composting process.

CRedit authorship contribution statement

Yingxin Li: Formal analysis, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Eiko E. Kuramae:** Project administration, Supervision, Writing – review & editing. **Yu Sun:** Writing – review & editing. **Chunjie Tian:** Project administration, Funding acquisition, Investigation, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biortech.2023.129132>.

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